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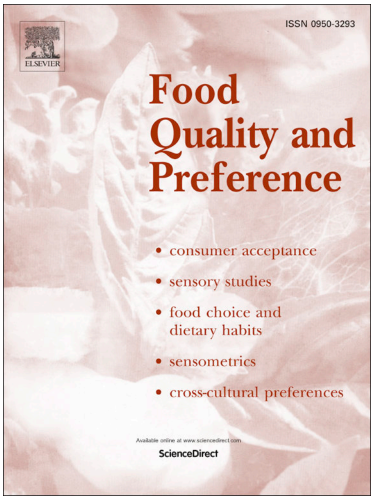

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Individual differences in responsiveness to oral sensations and odours with chemesthetic activity: relationships between sensory modalities and impact on the hedonic response

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Abstract

Independent sensory modalities are related and showed covariations in prior literature. However, little is known on the relationship between oral sensations and nasal chemesthesis. This large-scale study aims (I.) to test the hypothesis that response to oral stimuli is related to responsiveness to odours with chemesthetic activity; and (II.) to explore the implications of these relationships on liking.

Oral and olfactory responsiveness of 2205 Italians (18-65 years, men=41%) were evaluated. Intensities of tastes, astringency and pungency were collected in water solutions and in four foods modulated for target sensations. Responses to bitterness of 6-n-propylthiouracil (PROP) was measured. Odour intensity and irritation were assessed for three pure odorants (L-Menthol, trans-anethole, (+)-α-Terpineol) stimulating nasal chemesthesis (respectively: TRPM8, TRPA1, TRPA1). Liking for odours and foods was measured. Specific intensity indices were developed for each sensation.

Three clusters were identified based on taste intensity responses (Cl1, Cl2, Cl3). Cl1 (38%) was the most responsive to tastes, astringency, pungency, PROP and odours' intensity and irritation. This hyper-responsive cluster showed the highest hedonic variation (the span of liking ratings for stimuli with varied tastant concentrations). Cl2 (24%) was intermediate for oral responsiveness (apart for sourness) and Cl3 (38%) was the least responsive. Cl2 and Cl3 did not differ in odours' responsiveness (neither for perceived intensity nor for irritation). All sensory modalities were correlated but cross-correlations were higher when stimulating the same peripherical areas (oral vs oral more correlated than oral vs nasal). Results corroborate the idea of an overall high 'sensory responsiveness' covering different sensory modalities. Practical implications of the study are that less responsive subjects might require greater modifications in products formulations to modify their liking.

Keywords:

oral responsiveness, olfaction, nasal chemesthesis, irritant odorants, trigeminal nerve, liking

Highlights

- Subjects highly responsive to basic tastes are also highly responsive to astringency, pungency, PROP
- Oral responsiveness is related to responsiveness to odorants with trigeminal activity
- Oral irritation (capsaicin) and nasal irritation (odorants with chemesthetic activity) are correlated
- Hyper-responsive subjects have a higher hedonic variation (span in liking ratings)
- Less responsive subjects require greater modifications in products to modify their liking

1. Introduction

The perception of flavour is extremely complex, and it is the result of interactions across sensory modalities. Several associations between different sensory modalities have been shown in the literature (Braud & Boucher, 2020; Prescott & Stevenson, 2015). Odour perception and nasal chemesthesis are intimately connected (Tremblay & Frasnelli, 2018). In fact, most odorants are able to simultaneously stimulate olfactory and trigeminal systems in the nasal cavity (Abraham, Sánchez-Moreno, Cometto-Muñiz, & Cain, 2007; Brand, 2006; Doty et al., 1978). The physiology of olfaction and chemesthesis has been deeply described (Doty & Cometto-Muñiz, 2003; Patel & Pinto, 2014). Chemicals evoking nasal or oral chemesthesis have been routinely described as "trigeminal stimuli", since the nasal mucosa and the anterior regions of the oral cavity are both innervated by the trigeminal nerve (CN V) (Green, 2016). The olfactory system independently passes through the activation of the olfactory nerve (cranial nerve I) (Friedland & Harteneck 2017). Olfactory and trigeminal systems interact in the periphery at the mucosa level (Tremblay & Frasnelli, 2018). However, mechanisms by which specific odorants activate the trigeminal nerve are still largely undetermined (Richards, Johnson, & Silver, 2010).

The term 'chemesthesis' was early coined (Green, 1990) and it was defined as the chemical sensitivity of the skin and mucous membranes (not only in the mouth and nose). Chemesthesis has different functions, mostly related to warning systems (irritation, thermal activation, sense of pain, etc.), that is why the term 'chemofensor complex' was recently introduced meaning an 'array of defence mechanisms' that includes the chemesthesis (Green, 2012). Among the warning sensations, irritation is one of the major sensations mediated by chemesthesis. Irritation can arise in food due to the presence of different molecules like capsaicin in chilli peppers (Caterina et al., 1997), allicin in garlic or leek (Bautista et al., 2005; Gees et al., 2013; Macpherson et al., 2005), allyl isothiocyanate in wasabi and mustard (Engel, Martin, & Issanchou, 2006; Gerhold & Bautista, 2009), acetic acid in vinegar (Nielsen, 2018; Piochi, Cabrino, Morini, & Torri, 2020) or carbon dioxide in carbonated beverages (Iannilli, Del Gratta, Gerber, Romani, & Hummel, 2008) and many others. Sensation of irritation from food can be perceived in nose throughout volatile compounds (nasal irritation) or in the mouth due to non-volatile compounds (oral irritation). The two peripherical stimulation areas (nasal and oral) share the same activation of the trigeminal nerve. Nasal irritation has been described also as 'nasal pungency' which includes different sensations characterized by their sharp nature, such as 'stinging, freshness, prickling, piquancy, tingling, irritation, burning' (Abraham et al., 2007; Piochi et al., 2020). Oral irritation by compounds such as capsaicin has been mostly described by a 'burning/stinging' sensation (Karrer & Bartoshuk, 1991; Nolden, McGeary, & Hayes, 2016).

Considering the relationship between taste and chemesthesis, three experiments failed to find a significant association between oral chemesthesis (capsaicin, L-menthol) and taste (Green, Alvarez-Reeves, George, & Akirav, 2005), suggesting that these systems are independent. However, some studies found positive associations between basic tastes and chemesthetic (pungency) and tactile sensation (astringency) (Bajec & Pickering, 2008; Dinnella et al., 2018; Yang, Ma, Cao, Wang, & Zheng, 2014). Moreover, individuals who perceived taste from thermal stimulation alone (thermal tasters) gave significantly higher ratings to all taste stimuli in the evaluation of watery solutions (Green et al., 2005; Green & George, 2004). Thermal tasters reported stronger sensations in response to the olfactory stimulus vanillin (Green & George, 2004) suggesting that the responsiveness to different sensory modalities may be related.

To the best of our knowledge, few studies investigated the relationship between taste responsiveness and responsiveness to odour (Flaherty & Lim, 2017; Skrandies & Zschieschang, 2015). A limitation of these studies was the small samples used (<110). Noteworthy, a large-scale study has been recently conducted with the aim of assessing individual olfactory performance and changes in olfactory functionality in relation to specific age groups (Oleszkiewicz, Schriever, Croy, Hähner, & Hummel, 2019), but in this case relationships between olfaction and other sensory modalities were not considered.

In addition to the interactions occurring across sensory modalities, also the great inter-individual variability in responsiveness to sensory stimuli adds further complexity in the understanding of mechanisms contributing to the flavour perception. A high individual variability has been horizontally observed for odour responsiveness in food (Flaherty & Lim, 2017; Plotto, Barnes, & Goodner, 2006), for taste responsiveness (Bartoshuk, Duffy, & Miller, 1994; Dinnella et al., 2018; Lim, Urban, & Green, 2008) and for chemesthesis induced by both oral stimuli (Spinelli et al., 2018; Törnwall, Silventoinen, Kaprio, & Tuorila, 2012) and nasal stimuli (Engel et al., 2006; Piochi et al., 2020). Individual variability may also affect liking, choices, and food intake. For example, the contribution of taste responsiveness was documented in relationship to liking and choice of pungent foods (Spinelli et al., 2018) and in relationship to energy intake (Choi & Chan, 2015). Moreover, we recently showed that also individual variability to irritating stimuli affects the hedonic response in food naturally containing irritating substances (Piochi et al., 2020). Since individual preferences are related with specific eating patterns which have important nutrition implications (see for a review Diószegi, Llanaj, & Ádány, 2019), individual variability is important to explain food responses and behaviours.

Currently, the contribution of individual variability on food behaviours has been mostly studied considering one sensory modality at time (e.g. taste). However, considering ‘overall responsive subjects’ (instead of talking about subjects responsive to one specific sensory modality) seems more interesting to expand the picture. A previous review hypothesised to go beyond the concept of ‘supertasting’ for a specific molecule (e.g. PROP bitterness) and considered the possibility of thinking to a more inclusive and generical concept of overall ‘generalized supertasters’ (Hayes & Keast, 2011). Moreover, the relationships between individual variabilities in different sensory modalities (being a high/low responsive subject just in one or more sensory modalities) have been poorly studied, especially in large-scale studies handling wide representative pools (Piochi, Dinnella, Prescott, & Monteleone, 2018).

The relationship between intensity perception of sensory stimuli and liking has been studied since a long time (Moskowitz, 1982). It is known that the liking for food is affected by the perceived intensity of sensory stimuli in all sensory modalities, such as taste (Methven, Xiao, Cai, & Prescott, 2016; Thomas-Danguin, Guichard, & Salles, 2019), odour (Font i Furnols, Gispert, Diestre, & Oliver, 2003; Han et al., 2019) and oral chemesthesis (Piochi et al., 2020; Spinelli et al., 2018). However, the impact of covariations among sensory modalities, defined as different sensory modalities varying in a correlated way (intercorrelated sensory modalities), on liking is poorly studied.

Based on the fact that different sensory modalities seem related and that evidences exist that subjects responsive to a specific sensory modality may be also increasingly responsive to other sensory modalities, the current paper explores on a large-scale sample the following hypothesis: (I.) subjects phenotypically characterized by a high responsiveness to oral sensations are also characterised by a high responsiveness to odorants with chemesthetic activity and II. the differences in oral sensations and nasal chemesthetic impact on the hedonic response to these stimuli.

2. Materials and Methods

2.1 Study overview

The present study refers to the oral and the olfactory responsiveness data that were collected as part of the larger “Italian Taste” project, which was aimed at investigating influences on food choices and preferences in a large population sample (Monteleone et al., 2017). Data of the first two years of the project (during 2015 and 2016) were used. For a complete overview of the test and further details on the definition of the procedures, see (Monteleone et al., 2017). The procedure was approved by the ethics committee of Trieste University. Subjects took part in two sessions held in two days according to the Italian Taste project data collection scheme. At the time of recruitment, respondents signed the informed consent according to the principles of the Declaration of Helsinki and were introduced to the general organization of the study. Then they were asked to fill in an online questionnaire at home. On the first day in the lab, participants tasted and rated liking for four series of four samples modulated for target sensations; then the olfactory tests were performed and finally the responsiveness to PROP was measured. On the second day, intensity of seven water solutions and of target sensations in real food products were evaluated. Each session lasted approximately 2 hours each day. Designated breaks (10–15 min) between tests were carefully observed. In these breaks, participants were instructed on subsequent steps. Details for products, evaluation procedures and timing/breaks are given below.

2.2 Subjects

2205 Italians participated in the study (18-65 years, men=41%). Table 1 shows the characteristics of the population. Subjects were divided into three age classes (18–30; 31–45; 46–65 years). Data on socio-demographics information, smoking habits (*Never smoker*= Non-smoker; Former-smoker= *Not smoking now but have tried* or *quit*; Current smoker= *Yes Cigarette/Electronic cigarette/Pipe* or *cigar*) and chilli pepper and spicy food frequency of consumption were collected (8-point category scale then grouped into four classes: Never= *never;* rarely=*<1/month, 1–3/month;* Moderately=*1–2/week, 3–4/week;* Frequently= *5–6/week, 1/day, 2 +/day*). Subjects were also asked to declare how they judge their sense of smell (*lower than normal/ normal/ higher than normal*). Subjects declaring to have previously suffered from pathologies/alterations that can potentially compromise their sensory functionality (for examples otitis media, or problems in tastes or smells apart from commun cold) were found to be very few in a representative sub-sample of this pool (Dinnella et al. 2018).

Table 1

2.3 Oral responsiveness: taste and somatosensory stimuli

Water solutions and food products were used to assess responsiveness to tastes and somatosensory stimuli (Monteleone et al., 2017). Briefly, water solutions included five fundamental taste stimuli (citric acid 4 g/kg for sourness; caffeine 3 g/kg for bitterness; sucrose 200 g/kg for sweetness; sodium cloride 15 g/kg for saltiness; monosodium glutamic acid salt 10 g/kg for umami) and two somatosensory sensation stimuli (potassium aluminum sulfate 0.8 g/kg for astringency; capsaicin 1.5 mg/kg for pungency). Solutions (10 ml) were served in plastic cups, in balanced and randomized design. Pungency solution was always served as seventh sample, to avoid carryover effects due to the long duration of the pungency sensation. A 1 minute break was enforced between stimuli.

Products consisted in four series of four samples spiked with a tastant to elicit specific sensations (pear juice with 0.5; 2.0; 4.0; 8.0 g/kg citric acid for sourness; chocolate pudding with 38; 83; 119; 233 g/kg sucrose for sweetness; bean purée with 2.0; 6.1;10.7; 18.8 g/kg sodium chloride for saltiness; tomato juice with 0.3; 0.68; 1.01; 1.52 mg/kg capsaicin for pungency). Tomato juice, which is not a naturally spicy food, was chosen for spiking the capsaicin for several reasons, as the high familiarity of the Italian population with the pairing of tomato flavour and spiciness, the sensory stability, the easiness of use (manipulation and spiking) and the availability of the commercial tomato juice on national scale. In each food series, ‘C1’ and ‘C4’ identified in the text respectively the lowest and the highest target stimulus concentration. The food product series (15g for each sample) were presented in independent sets, each consisting of four samples of the same product. Within the series, the four levels of target stimulus were presented in random order, while the order of the series was fixed (pear juice; chocolate pudding; bean purée; tomato juice). A 10 minute break was enforced after the pear juice series and after the bean cream set, while a 15-minute break was observed between chocolate pudding and bean purée. Whitin each series, a 1 minute break was observed among samples representing different levels of the stimulus. Responsiveness to bitterness of 6-n-prophyl thiouracyle (PROP) was assessed as an oral responsiveness index. The two-solution procedure was adopted (Monteleone et al., 2017), in which subjects evaluated in duplicate a 3.2 mM PROP solution of 6-n-propyl-2-thiouracil (Sigma-Aldrich) prepared dissolving 0.5447 g/L PROP into deionized water. Subjects were instructed to hold each sample (10 ml) in their mouth for 10 s and expectorate, and then wait 20 s before evaluating the intensity of bitterness. Subjects had a 90 s break between the two samples. Subjects were classified for responsiveness to PROP bitterness into three classes applying previously used cut-off values (Fischer et al., 2013): non-taster=NT (ratings on gLMS ≤ moderate, 17), medium-taster=MT (17 < ratings on gLMS < 53), and super-taster=ST (ratings on gLMS ≥ very strong, 53).

All samples were codified with a random three digit-code number. All oral intensities were estimated using the Generalized Labeled Magnitude Scale (0=no sensation; 100=the strongest imaginable sensation of any kind) (Bartoshuk et al., 2004). Subjects were extensively instructed in the use of the scale. They were instructed to treat the ‘‘strongest imaginable sensation” as the most intense sensation they can imagine involving remembered/imagined sensations in any sensory modality, including non-oral sensations, such as loudness, oral pain/irritation, or sight (e.g., the loudest sound ever heard, the most intense pain experienced, or the brightest light ever seen). Among these examples, we used the evaluation of the brightest light they had ever seen to include/ exclude subjects. In particular, the criterion to conclude that subjects correctly used the scale was that ratings for the brightest light ever experienced must have been higher than very strong but lower than the strongest imaginable. Liking for food products was assessed with the use of the Labeled Affective Magnitude scale (0=the greatest imaginable dislike, 50=neither dislike nor like, 100=the greatest imaginable like (Schutz & Cardello, 2001).

2.4 Olfactory responsiveness: odour stimuli

Three pure odorants (mint, anise, pine) stimulating nasal chemesthesis were tested: L-Menthol stimulating the TRPM8 transient receptor potential ion channels (Weyer-Menkhoff & Lötsch, 2018), trans-anethole stimulating the TRPA1 (Richards et al., 2010), and (+)-α-Terpineol stimulating the TRPA1 (Richards et al., 2010). The odours were selected from the ones included in the European Test of Olfactory Capabilities (Joussain et al., 2015) and presented using cardstocks designed for the project ‘‘La Prévalence des troubles Olfactifs en France” (Projet DEFISENS – PREVAL – OLF) coordinated by Moustafa Bensafi (CRNL, Lyon, France) who kindly provided the material. Odorant molecules were trapped in tight microcapsules (aminoplast type, diameter: 4–8 micro). The microcapsule-based ink was printed on a cardstock (SILK-250 g; Dimension: 11 cm x 21 cm). Each odorant was printed on a delimited area (2-cm diameter disc). The release of the odour was done simply by rubbing the printed microcapsule reserve. Liking, intensity and irritation were measured for each odour. Odour liking was evaluated on a 9-point hedonic scale (1 = extremely disliked; 9 = extremely liked) (Peryam & Pilgrim, 1957). Odour intensity and odour irritation were collected on 9-point scales (1=extremely weak, 9=extremely strong; 1=not at all irritant, 9=extremely irritant). Discrete scales has been previously used for odour intensity quantification (Licon et al. 2018; Ramalho, Jacquelin, and Maupetit 2003). Since in general the sense of taste is qualitatively simpler than olfaction (Lawless 1991) and odour intensity seemed to be reliably quantified both by linear scales and discrete scales (Ramalho, Jacquelin, and Maupetit 2003), 9-point scales were chosen for the odour evaluation as a good compromise between easiness of use and reliability.The odorants were presented in a randomized order and a 1 minute break was observed between each odorant.

2.5 Data analysis

One-way ANOVA models (fixed factor: year) were used to assessed the effect of the project year on the intensity perceived of each odour to check for the stability of odorants.

Intensity indices were specifically computed, each one relevant to one sensation (Table 2) Each index was obtained for each subject by summing up the intensity ratings given to the sensation evaluated in different stimuli (such as water solutions, food or in odours). For example, the 'Sour_Index' was estimated for each subject by summing up five measurements of sourness: the rating given to sourness in water solution and four sourness ratings evaluated in the respective four acidified pear juices. Ten indices were computed in total: Salty_Index, Sour_Index, Sweet_Index, Bitterness_Index, Umami_Index, Tastes_Index, Astringency_Index, Pugency_Index, Odour_Intensity_Index, and Odour_Irritation_Index.

Table 2

To have a configuration of subjects based on their basic tastes responsiveness, a Principal Component Analysis (PCA) was conducted on the five Indices for tastes (Salty_index; Sour_index; Sweet_Index; Bitterness_Index; Umami_index) individually obtained for all subjects. A segmentation (Agglomerative hierarchical clustering AHC; centering and reducing data; Dissimilarity: Euclidean distance; Agglomeration method: Ward's method) was applied to factor scores of the first four principal component (PCs) of the PCA, obtaining three clusters. The selection of the PCs was done according to the broken stick criterion (Jolliffe, 1986). One-way ANOVA models were used to estimate the effect of cluster on responsiveness to intensities and irritation both given to single sensations and to Intensity Indices (fixed factor: cluster), followed by Tukey's HSD tests ($p<0.05$). Two-way ANOVA models (fixed factors: cluster, product concentration level; models with interactions) were separately calculated to assess the effect of cluster on perceived intensity of target sensations and liking of products.

Differences in the composition among clusters in terms of gender, numerosity in age classes, smoking status, frequency of spicy food consumption, self-reported sense of smell and PROP status were assessed with Chi-square tests followed by Fisher's exact tests ($p<0.05$). R Pearson coefficient was used to assess the relationships among variables in the total population ($p<0.05$).

For each subject, a delta intensity and a delta liking were computed for each product.

The delta intensity (Δ INT std) was calculated as follows on standardized data (Z score matrices):

Δ INT std = (standardized score given to the sample with the highest level C4) – (standardized score given to the sample with the lowest level C1)

Δ INT std was an estimation in absolute value of the span in the variation of the perceived intensity of a stimulus with varied concentrations in the same matrix (perceived intensity variation). Δ INT std shows how a subject was sensitive/non sensitive to that stimulus: the highest the Δ INT std, the highest the variation in perceived intensity and therefore the highest the sensitivity to that stimulus variation by that subject.

Similarly, the delta liking (Δ LIK) was calculated on original data as follows:

Δ LIK = (liking score given to the most liked sample) – (liking score given to the least liked sample)

Δ LIK was an estimation in absolute value of the hedonic variation of the subject, defined as the span in liking from the most to the least liked sample: higher Δ LIK indicated a higher variation in the hedonic response, therefore greater changes in liking ratings when varying the concentrations of a target stimulus in the same matrix. One-way ANOVA models (fixed factor: cluster) followed by Tukey's HSD test were separately used to assess the effect of the cluster on the variation in perceived intensity and in the hedonic variation for each product.

3. Results

3.1 Variables' distribution in the population and correlations across modalities

The perceived intensities of stimuli in water solutions in the total population ranged from 'moderate' (17) to higher than 'strong' (45) with the following medians: 17 (astringent), 22 (umami), 29 (bitter), 31 (sour), 35 (salty), 36 (sweet), pungent (45). In food products, two-way ANOVA models showed a significant effect ($p<0.05$) of the concentration on the intensity ratings for each product type in the expected direction (C4>C3>C2>C1), confirming that prototypes have been prepared in a way that allowed to have a significant increase in perceived intensity of each target sensation.

No significant effect ($p>0.05$) of the project year was found on the intensity of the three odorants (mint: F=0.85; anise: F=0.07; pine: F=0.04), suggesting that all three odorants were stable over the two considered years.

Correlations among Indices are shown in Table 3. Intensity_Indices were all positively ($p<0.001$) correlated to each other.

Table 3

The bi-plot from PCA shown in Figure 1 represents the characterization of subjects in relationship to their taste intensity Indices. The first four PCs accounted for 92.8% of the total variability. PC1 (60% of the total variance) mainly discriminated subjects according to intensities increasing for all taste intensity_Indices along PC1 (Fig. 1a). PC2 (12.5%) discriminated subjects mainly according to the type of taste sensations, with Bitter_Index and Sour_Index having positive loadings and Umami_Index, Salty_index and Sweet_Index having negative loadings on PC2 (Fig. 1a). The variables distribution on PC2 tended to be grouped according to taste qualities innately liked (like sweet, salty and umami; negative loadings on PC2) and warning sensations (like sour and bitter; positive loadings on PC2) (Reed & Knaapila, 2010). Along PC3 (accounting 11% of the total variance) and PC4 (9.3%), the Intensity indices were quite scattered (therefore showing different correlation loadings) (data not shown).

Along PC3, Umami_Index showed an opposite correlation with Sour_Index (Fig. 1b). On PC4, two groups of variables with different loadings (negative vs positive) were observed (Bitter_Index, Salty_Index and Sweet_Index vs Umami_Index and Sour_Index).

Figure 1a, 1b

3.2 Cluster characterization

From the subjects' segmentation, three clusters were identified (Cl1=38%, Cl2=24%, Cl3=38%). A strong effect of the cluster ($p<0.001$) was found for all intensities of taste sensations perceived in water solutions (sour, bitter, sweet, salty, umami) and the derived Intensity_Indices (Table 4). Cl1 gave the significantly highest ratings (at least 'strong') to all considered tastes, while Cl3 gave the lowest ratings (around 'moderate') to all the considered tastes except for sourness. Cl2 was the intermediate and the least responsive for sourness. For somatosensory sensations, congruently to what observed for tastes, Cl1 gave the highest intensities both to astringency and pungency, Cl2 intermediate and Cl3 the lowest intensities.

Table 4

Results of the responsiveness to olfactory stimuli from clusters are shown in Table 5. The cluster had a significant effect ($p<0.001$) on all types of odour. Cl1 gave significantly higher ratings to odour intensities, odour irritations and to the related Odour_Intensity_Index and the Odour_Irritation_Index. Ratings given by Cl2 and Cl3 did not significantly differ.

Table 5

No differences were found across clusters for gender, age, smoking status, frequency of consumption of spicy food and self-reported sense of smell. Instead, the Chi-square test showed a clear different distribution in PROP classes across the three clusters. Fisher's exact test showed that Cl1 had a significantly higher number of ST (40%) than expected and a lower number of MT and NT. Instead, Cl3 had a significantly higher number of NT (29%) and MT (51%) than expected (Table 1).

3.3 Effect of cluster on the perceived intensity variation (Δ INT std) and on the hedonic variation (Δ LIK)

The effect of cluster on the perceived intensity variation of oral stimuli in real products is shown in Figure 2. Clusters significantly ($p<0.001$) differ from each other in the extent of perceived difference in sourness in pear juice ($F=28.48$), sweetness in chocolate pudding ($F=49.40$), saltiness in bean purée ($F=31.01$) and pungency in tomato juices ($F=6.62$). Cl1 was the most sensitive cluster to changes in product stimuli concentrations (greater Δ INT std values for all products), while Cl3 was the least sensitive for sweetness. Cl3 tended also to have the lowest Δ INT std for saltiness (bean purée) and pungency (tomato purée), without significant differences from Cl2. Thus, Cl3 confirmed to be the least responsive.

Figure 2

The effect of cluster on the hedonic variation evaluated for real products is shown in Figure 3. A significant effect (p<0.001) of the cluster was found in liking for all products in which one target sensation was modulated: sourness (F=21.46, pear juice), sweetness (F=25.06, chocolate pudding), saltiness (F=31.50, bean purée) and pungency (F=15.88, tomato juice). Cl1 exhibited the highest hedonic variation across all products, having the greatest liking span when considering the most preferred to the least liked samples. Cl2 and Cl3 showed the same hedonic variation for pear juice, bean purée and tomato juice, while Cl2 had a higher liking span in the case of chocolate pudding, not significantly different from Cl1.

Figure 3

4. Discussion

4.1 Relationship between oral sensations and nasal chemesthesis

In the current paper a positive relationship was observed between responsiveness to oral sensations and responsiveness to odorants with chemesthetic activity, confirming the first hypothesis.

To assess whether subjects highly responsive to taste stimuli were also highly responsive to odorants with chemesthetic activity, subjects were firstly segmented based on their taste responsiveness, using specifically developed intensity indices based on responsiveness to taste. Three clusters were obtained. One cluster clearly gave the highest ratings for all taste qualities (Cl1), Cl2 was intermediate except for sourness and Cl3 the least taste responsive. The reduced responsiveness of Cl2 to sourness is hard to explain with data available in the current study. It is known that sour taste is detected by the taste system (type III taste cells in taste buds responding to acid taste stimulation by releasing serotonin) (Huang, Maruyama, Stimac, & Roper, 2008) and it was recently found that Transient Receptor Potential (TRP) channel TRPV4 also contributes to sour taste sensing (Matsumoto et al., 2019). Previous studies showed alteration in sourness responsiveness in patients with Crohn's disease (Szymandera-Buszka, Jędrusek-Golińska, Waszkowiak, & Hęś, 2020). However, we did not find any study reporting reduced sourness perception in healthy subjects apart from studies focusing on the suppression or partial masking of sourness through mixtures (Savant & McDaniel, 2004).It is plausible that differences in sourness could be related to variables that were not considered in the current study (such as the familiarity towards sour food).

Cl1 proved to be also the most responsive to astringency and pungency, therefore showing an overall high responsiveness which interested all oral sensations, including tastes, and PROP with the highest percentage of supertaster (40%). This percentage is high if compared to the percentage of supertasters in Caucasian population of approximately 25% (Bartoshuk et al., 1994), even considering potential overestimation of PROP ST due to different systems of classification. Since responsiveness to PROP is considered an important phenotypic marker of taste responsiveness (Bartoshuk et al., 1994; Tepper, Banni, Melis, Crnjar, & Barbarossa, 2014), the fact that the most responsive group has a high percentage of PROP ST corroborates the hypothesis of a generical hyper-responsiveness of this group. This was previously suggested referring to the PROP and the term “supertasting” should extend beyond supertasting of PROP bitterness to other tastants including oral somatosensation and retronasal olfaction (Hayes & Keast, 2011). Moreover, the higher oral responsiveness of Cl1 translated into a higher olfactory responsiveness (both including odour intensity and odour irritation), thus confirming our hypothesis of the existence of a group with generalized overall heightened responsiveness. Since, a previous study suggested that the individual differences in thermal taste perception were associated with a generally higher responsiveness to both gustatory and olfactory stimulation (Green & George, 2004), it would be interesting to assess whether the most responsive subjects (Cl1) would be also highly responsive to the thermal stimulation (therefore showing a higher amount of thermal tasters). Moreover, since the perception of texture varies among individuals (Hayes & Duffy, 2007) and subjects differ in oral tactile acuity (Cattaneo, Liu, Bech, Pagliarini, & Bredie, 2020; Essick, Chopra, Guest, & McGlone, 2003), it would be interesting to explore the relationship with oral and nasal responsiveness also in respect to tactile acuity.

Demographic factors, such as age and gender (Wang, Liang, Lin, Chen, & Jiang, 2020; Zhang & Wang, 2017), and oral-related food behaviours, such as smoking habits (Ajmani, Suh, Wroblewski, & Pinto, 2017) and spicy food consumption, may be related to sensory responsiveness,. From the characterization of the three clusters, the groups were substantially homogenous for most considered variables (gender composition, age, smoking habits, frequency of consumption of spicy food and self-reported sense of smell). Thus, it is possible to hypothesise that observed differences in responsiveness across clusters were mostly linked to the different sensory acuity rather than environmental factors. However, it is also possible that clusters differ in other variables as psychological traits or attitudes that have been found to influence both liking and perception and that were not examined here (De Toffoli et al., 2019; Laureati et al., 2018; Spinelli et al., 2018; Ullrich, Touger-Decker, O'sullivan-Maillet, & Tepper, 2004). For example, we might hypothesize that traits that were associated with a heightened perception of the pungency induced by capsaicin such as neophobia, sensitivity to disgust and to punishment (Spinelli et al., 2018) characterize the hyper-responsive cluster or that the lower hedonic variation in hypo-responsive cluster is due to a lower impact of the critical sensory properties, in agreement with previous studies (De Toffoli et al., 2019; Laureati et al., 2018).

In the current study, all considered sensory modalities were found to be positively correlated to each other in the population with low to modest values of correlation. The highest correlations were found among Taste_Index and the somatosensory sensations (astringency and pungency), indicating a clear covariation of the oral sensations when the peripherical stimulation has the same localization (oral). These values are in line with previously observed correlations reported in literature for taste qualities, which ranged from low to modest correlations (Pearson R from 0.2 to 0.5) (Dinnella et al., 2018; Lim et al., 2008; Webb, Bolhuis, Cicerale, Hayes, & Keast, 2015). In addition, Pungency_Index and Astringency_Index were significantly correlated to each other with a correlation value (R=0.34) which was higher than what previously observed among these two sensations (R=0.195) (Dinnella et al. 2018).

A previous study found that thresholds for odours and sweet or salty taste were correlated (Skrandies & Zschieschang, 2015), suggesting a covariation between taste and olfaction. In the current study, the correlations between systems with a different peripherical anatomical localization (oral vs nasal, like for example Taste_Index vs Odour_Intensity_Index) were lower but still significant. This result is in full agreement with a recent study which found higher correlations between modalities than across modalities (Flaherty & Lim, 2017). In addition, the two sensations related to irritation (Pungency_Index and Odour_Irritation_Index) were positively correlated to each other. This last result may be explicated by the fact that both modalities stimulate the trigeminal nerve. In fact, it is well know that capsaicin stimulates TRPV1 (Weyer-Menkhoff & Lötsch, 2018), which is a heat-activated ion channel in the pain pathway (Caterina et al., 1997) eliciting a burning sensation in mouth, and the three odorants activate Transient Receptors Channels (TRC) in the nasal cavity (respectively: L-Menthol TRPM8, trans-anethole the TRPA1, and (+)-α-Terpineol the TRPA1) (Richards et al. 2010; Weyer-Menkhoff and Lötsch 2018). Finally, as previously observed in food models containing natural irritants (Piochi et al., 2020), in the current study Odour_Intensity_Index was positively correlated with Odour_Irritation_Index.

Two scenarios have been envisaged regarding the covariation among different sensory modalities (meant as different sensory modalities varying in a correlated way): either 1. the presence of a 'compensatory system' in individuals (a high responsiveness to one of the two sensory modalities compensates for the low responsiveness in the other sensory modality); or 2. a 'reinforced system' (subjects highly responsive to one sensory modality showed increased responsiveness also in the other modality), which may be due not only to the peripheral innervation but also to specific central neural process ("central gain" theory) (Green & George, 2004).Results of current paper rather reinforces the latter scenario, showing the presence of a cluster (Cl1) highly responsive for all stimuli . Findings are in line with a review that suggests the use of the term 'hypergeusia' for subjects highly responsive to PROP bitterness and in general to different stimuli (Hayes & Keast, 2011) and with previous studies founding that basic tastes were correlated (Puputti, Aisala, Hoppu, & Sandell, 2018; Webb et al., 2015).

4.2 Impact of the variability in oral responsiveness and nasal chemesthesis on liking

The differences in responsiveness to oral sensations and nasal chemesthetic impact on liking, as hypothesised. Subjects with the highest oral and nasal responsiveness (Cl1) showed the highest perceived intensity variation (Δ INT std). The higher Δ INT std of Cl1 translated into a higher hedonic variation, indicating that more responsive subjects had greater liking changes when modifying the products formulations. This finding is in line with an extended literature highlighting how sensory responsiveness (both including taste or olfactory responsiveness) influences the hedonic responses (Jaeger et al., 2013; Masi, Dinnella, Monteleone, & Prescott, 2015; Piochi et al., 2020). These results suggest that highly responsive subjects perceive smaller variations in food products composition more easily, therefore they could require smaller formula changes in order to have a variation in liking, in contrast to low sensory responsive subjects. Product developers should consider this aspect and take advantage of it, both considering the starting level of liking of the product (either if low or moderate/high) and the target to which the product is addressed. Examples of specific targets with reduced oral responsiveness who may require stronger formula modifications to improve their liking are overweight/obese people keeping constant the caloric contribution at low levels (Proserpio, Laureati, Bertoli, Battezzati, & Pagliarini, 2016; Vignini et al., 2019) or the elderly in the field of food improvement intervention for the development of palatable food (Abbott et al., 2013; Forde & Delahunty, 2004). On the other hand, if the level of acceptability is already moderate/high among the low responsive, they may be more tolerant to modifications of formulation, since their liking does not change that much. In a wider framework, these findings may have important practical implications in the field of product's optimization and meal development for specific target of subjects that have a reduced taste responsiveness.

5. Conclusions

The present paper explored on a large scale the hypothesis that subjects highly responsive to oral stimuli are also highly responsive to odorants with chemesthetic activity and it explored the impact of these relationships on sensory responsiveness and on the hedonic response. Results demonstrated that subjects highly responsive to tastes were highly responsive to somatosensory stimuli (astringency and pungency), to PROP and to odour intensity and irritation. Oral irritation (by capsaicin) and nasal irritation (by odorants with chemesthetic activity stimulating different TRCs) were correlated, even if weakly. Taken together, these findings reinforce the idea of a generical phenotypical 'hyper-sensory-responsive' group, showing high responsiveness in all sensory modalities. Correlations between sensations perceived in oral cavity were stronger (taste with oral pungency and astringency) than those among sensations having different peripherical stimulation (oral vs nasal). The highest sensory responsiveness was clearly associated with the highest hedonic variation. The practical implications of these findings rely to product's optimization: results suggest that subjects poorly responsive to sensory stimuli (oral and olfactory) may therefore require greater formula modifications in products to effectively modify their liking.

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Author contributions

MP and LT structured the analyses' and the manuscript scaffold. MP undertook the analyses and wrote the manuscript. CD crucially contributed to enrich the analyses. LT essentially contributed to revise the manuscript. EM, SS, CD, and LT originally collaborated in the design of the project Italian Taste. All authors discussed the interpretation of the results, helped with data collection, reviewed, and offered critical comments on the manuscript.

Declaration of Competing Interest

The authors confirm that there are no financial contributions to the work and no potential conflicts of interest to declare.

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Tables

Table 1. Characteristics of the total population and of each cluster.

Variables	**Total (n=2205)**		**Cl1 (n=846, 38%)**		**Cl2 (n=522, 24%)**		**Cl3 (n=837, 38%)**		**χ^2 across clusters**		
	N.	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**χ^2**	**DF**	**P**
Gender											
Women	1301	59	493	58	306	59	502	60	1.54	2	0.76
Men	904	41	353	42	216	41	335	40			
Age (years)											
18-30	834	38	340	40	209	40	285	**34** <	8.18	2	0.09
31-45	629	29	232	27	143	27	254	30			
46-65	742	34	274	33	170	33	298	36			

Smoking status													
Never-smokers	1252	57	466	55		305	59	481	58		5.05	4	0.28
Former-smokers	406	18	148	18		95	18	163	19				
Current smokers	540	24	228	**27**	**>**	120	23	192	23				
Frequency consumption of spicy food*													
Never	305	14	104	12		86	16	115	14		7.30	6	0.29
Rarely	1183	54	453	54		268	51	462	55				
Moderately	585	27	233	28		134	26	218	26				
Frequently	130	6	54	6		34	7	42	5				
Self-reported sense of smell													
Lower than normal	88	4	35	4		24	5	29	3		6.87	4	0.14
Normal	1819	83	678	**80**	**<**	431	83	710	**85**	**>**			
Higher than normal	296	13	131	**16**	**>**	67	13	98	12				
PROP status													
NT	541	25	186	**22**	**<**	115	22	240	**29**	**>**	78.35	4	<0.001
MT	996	45	323	**38**	**<**	246	47	427	**51**	**>**			
ST	668	30	337	**40**	**<**	161	31	170	**20**	**<**			

*Rarely = max once per month; Moderately (1-4 times per week); Frequently (≥5 times per week).

NT, MT and ST indicate respectively PROP non-taster, PROP medium-taster and PROP supertaster.

Values and signs “>” or “<”in bold type indicate respectively a significantly higher and lower than expected percentage of subjects classified as the corresponding sub-class for each cluster, from Fisher’s exact test (p<0.05).

Table 2. Intensity Indices computed for all the sensory stimuli included in each Intensity_Index.

Intensity Index	**N. ratings included in the index**	**Type of ratings and stimuli considered to compute the index**
Salty_Index	5	Sum of the perceived intensity of saltiness in water solution and in four bean purées
Sour_Index	5	Sum of the perceived intensity of sourness in water solution and in four pear juices
Sweet_Index	5	Sum of the perceived intensity of sweetness in water solution and in four chocolate pudding
Bitter_Index	5	Sum of the perceived intensity of bitterness in water solution and in four chocolate puddings
Umami_Index	5	Sum of the perceived intensity of umami in water solution and in four bean purées
Taste_Index	5	Sum of the perceived intensities of five sensations in water solutions: sourness, bitterness, sweetness, saltiness, umami.
Astringency_Index	5	Sum of the perceived intensity of astringency in water solution and in four chocolate puddings
Pungency_Index	5	Sum of the perceived intensity of pungency in water solution and in four tomato juices
Odour_Intensity_Index	3	Sum of the perceived odour intensities of three pure odorants (mint, anise, pine)
Odour_Irritation_Index	3	Sum of the perceived odour irritation for three pure odorants (mint, anise, pine)

Table 3. Pearson correlation matrix among responsiveness Indices in the total population (n=2205).

Variables	Odour_Intensity_index	Odour_Irritation_Index	Tastes_Index	Pungency_Index	Astringency_Index
Odour_Intensity_index	**1**				
Odour_Irritation_Index	**0.18**	**1**			
Taste_Index	**0.15**	**0.08**	**1**		
Pungency_Index	**0.08**	**0.10**	**0.43**	**1**	
Astringency_Index	**0.12**	**0.17**	**0.45**	**0.34**	**1**

Values in bold are different from 0 with a significance level alpha=0.05

Table 4. Cluster effects on intensity ratings of oral sensations in water solutions and on the related oral Intensity Indices.

Data	Variables	Cl 1	Cl 2	Cl 3	F	p-value
Intensity ratings	sourness	45.4± 0.6 a	25.2± 0.8 c	27.7± 0.6 b	266.02	< 0.001
	bitterness	42.3± 0.7 a	29.3± 0.8 b	22.8± 0.7 c	219.31	< 0.001
	sweetness	52.7± 0.6 a	37.5± 0.7 b	28.9± 0.6 c	457.68	< 0.001
	saltiness	49.0± 0.6 a	36.6± 0.8 b	27.0± 0.6 c	321.7	< 0.001
	umami	34.4± 0.6 a	28.7± 0.8 b	18.4± 0.6 c	181.63	< 0.001
	astringency	25.1± 0.6 a	17.6± 0.7 b	14.4± 0.6 c	88.96	< 0.001
	pungency	54.6± 0.7 a	44.6± 0.9 b	39.4± 0.7 c	106.47	< 0.001
Intensity Indices	Tastes_Index	223.7± 1.9 a	157.3± 2.5 b	124.7± 1.9 c	668.21	< 0.001
	Sour_Index	153.8± 1.5 a	75.2± 1.9 c	90.1± 1.5 b	654.73	< 0.001

	Bitter_index	138.4± 1.4 a	95.7± 1.8 b	71.5± 1.4 c	548.26	< 0.001
	Sweet_index	151.0± 1.1 a	104.5± 1.4 b	78.7± 1.1 c	1032.91	< 0.001
	Salty_Index	160.7± 1.3 a	118.6± 1.7 b	84.3± 1.3 c	861.08	< 0.001
	Umami_Index	114.6± 1.4 a	101.4± 1.8 b	54.5± 1.4 c	474.85	< 0.001
	Astringency_Index	87.6± 1.4 a	57.9± 1.8 b	41.7± 1.4 c	272.57	< 0.001
	Pungency_Index	178.5± 2.0 a	139.3± 2.6 b	118.1± 2.1 c	220.87	< 0.001

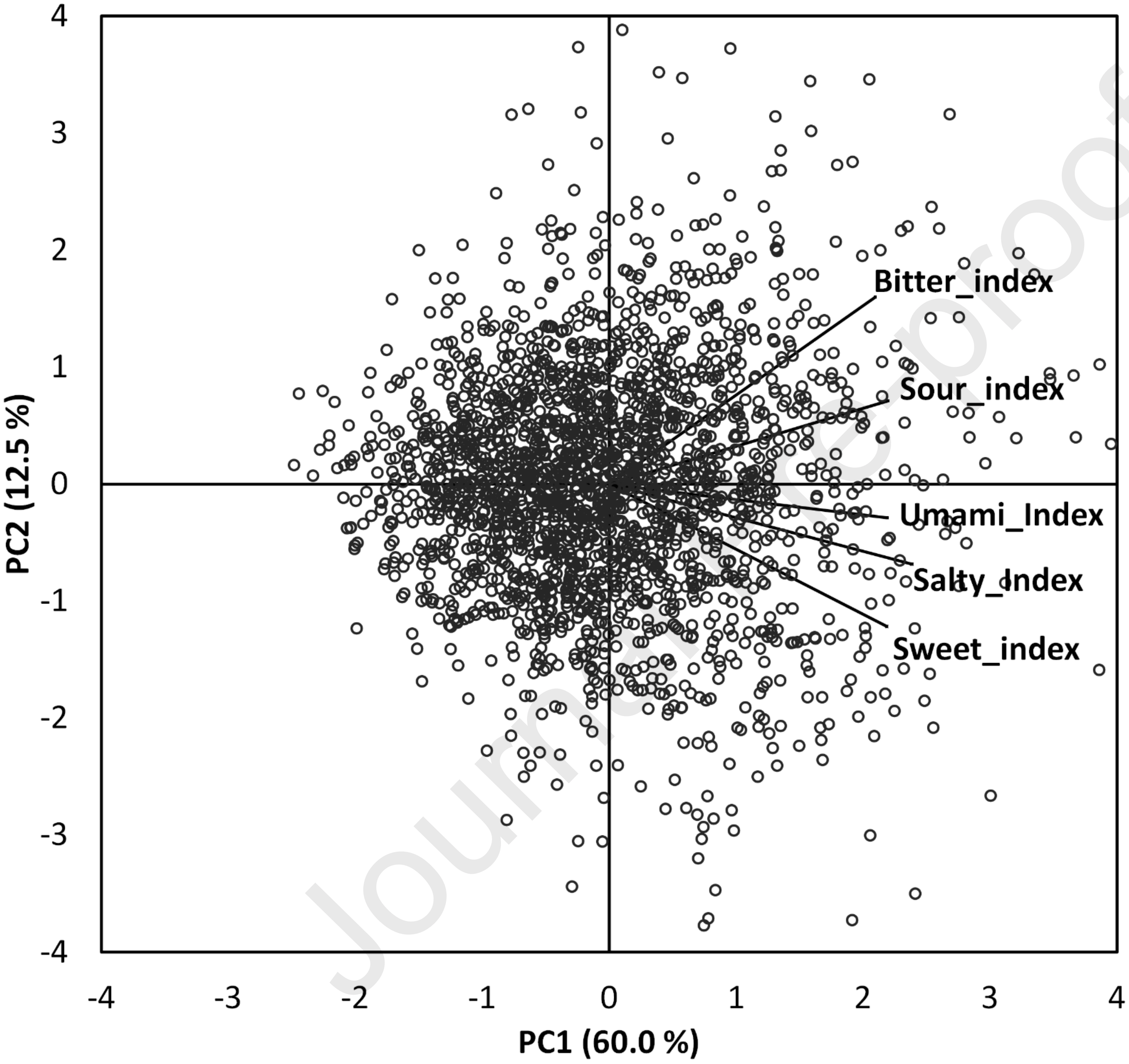
Note: different letters in rows indicate significant (p<0.05) different mean values from Tukey's HSD test.

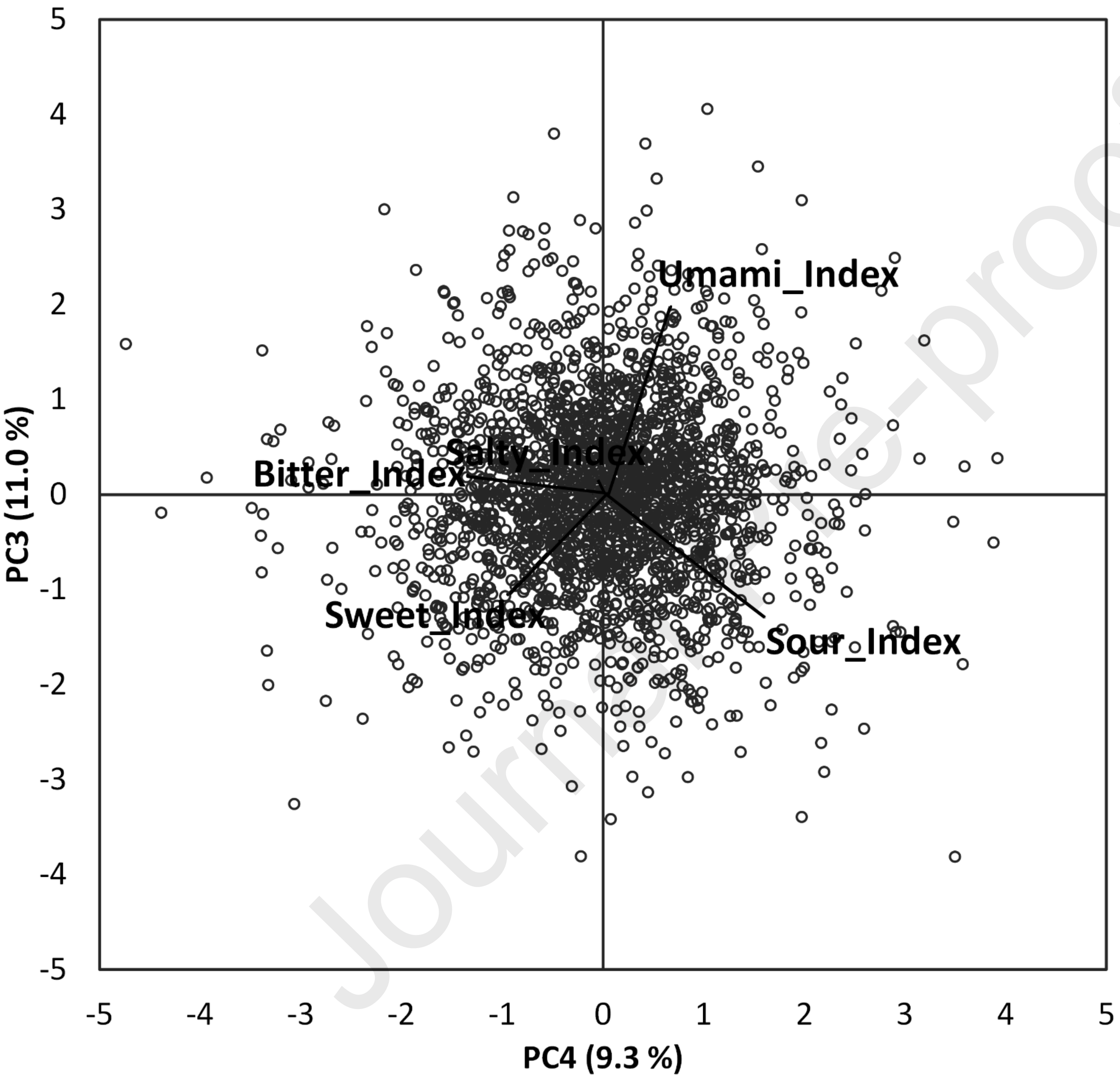
Table 5. Cluster effects on nasal intensity and irritating ratings of three odorants and on the related odour Intensity Indices.

Data	Variables	Cl 1	Cl 2	Cl 3	F	p-value
Intensity ratings	Intensity_Mint	6.3± 0.1 ^{a}	6.0± 0.1 ^{b}	5.9± 0.1 ^{b}	11.76	< 0.001
	Intensity_Anise	5.2± 0.1 ^{a}	4.7± 0.1 ^{b}	4.9± 0.1 ^{b}	12.44	< 0.001
	Intensity_Pine	6.4± 0.1 ^{a}	5.9± 0.1 ^{b}	5.9± 0.1 ^{b}	19.12	< 0.001
	Irritation_Mint	2.0± 0.1 ^{a}	1.7± 0.1 ^{b}	1.6± 0.1 ^{b}	10.17	< 0.001
	Irritation_Anise	2.0± 0.1 ^{a}	1.9± 0.1 ^{ab}	1.8± 0.1 ^{b}	5.33	< 0.001
	Irritation_Pine	2.8± 0.1 ^{a}	2.4± 0.1 ^{b}	2.3± 0.1 ^{b}	12.83	< 0.001
Intensity Indices	Odour_Intensity_index	17.9± 0.1 ^{a}	16.6± 0.2 ^{b}	16.7± 0.1 ^{b}	24.97	< 0.001
	Odour_Irritation_Index	6.8± 0.1 ^{a}	6.1± 0.2 ^{b}	5.7± 0.1 ^{b}	14.99	< 0.001

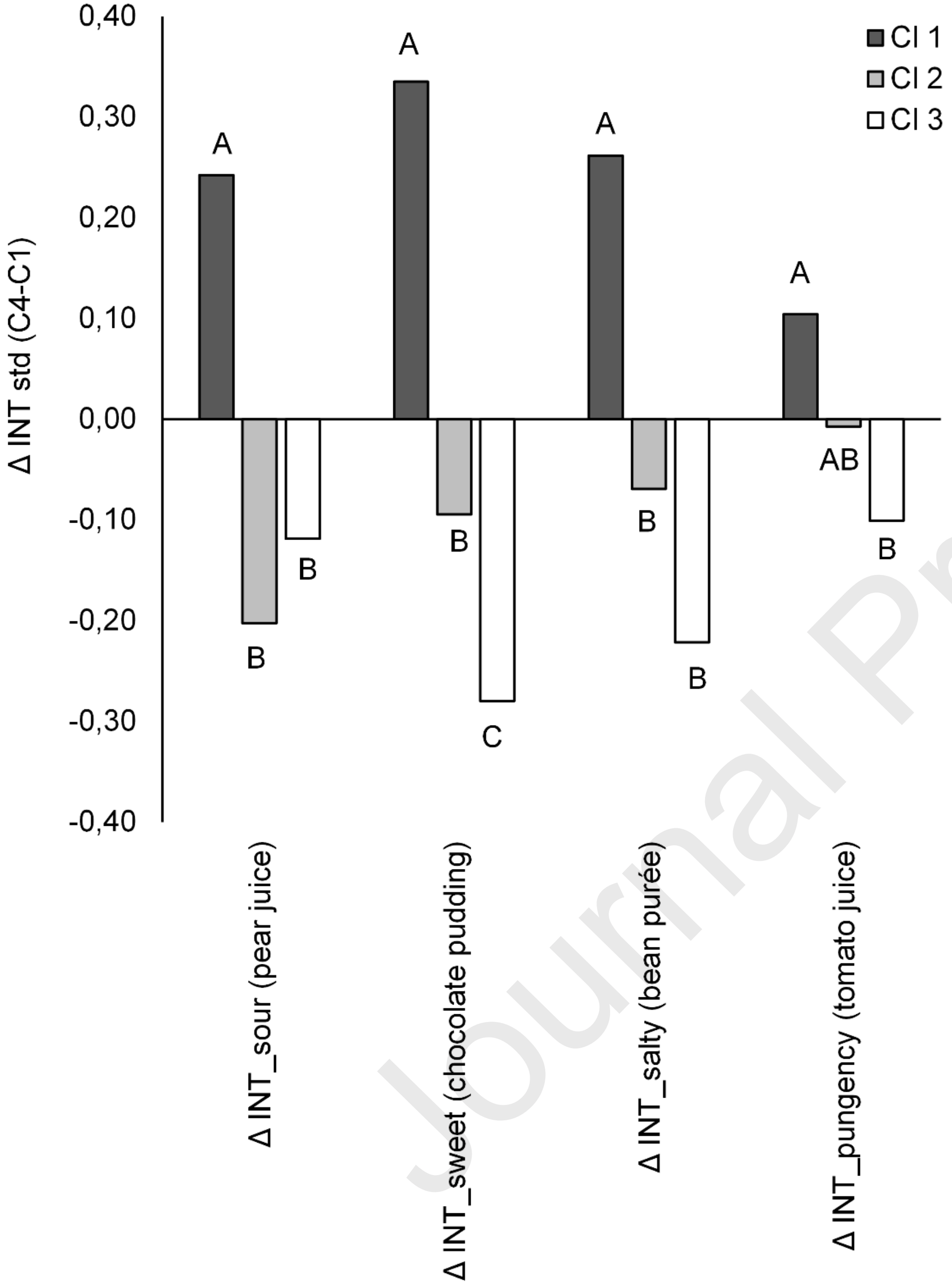
Note: different letters in rows indicate significant (p<0.05) different mean values from Tukey's HSD test.

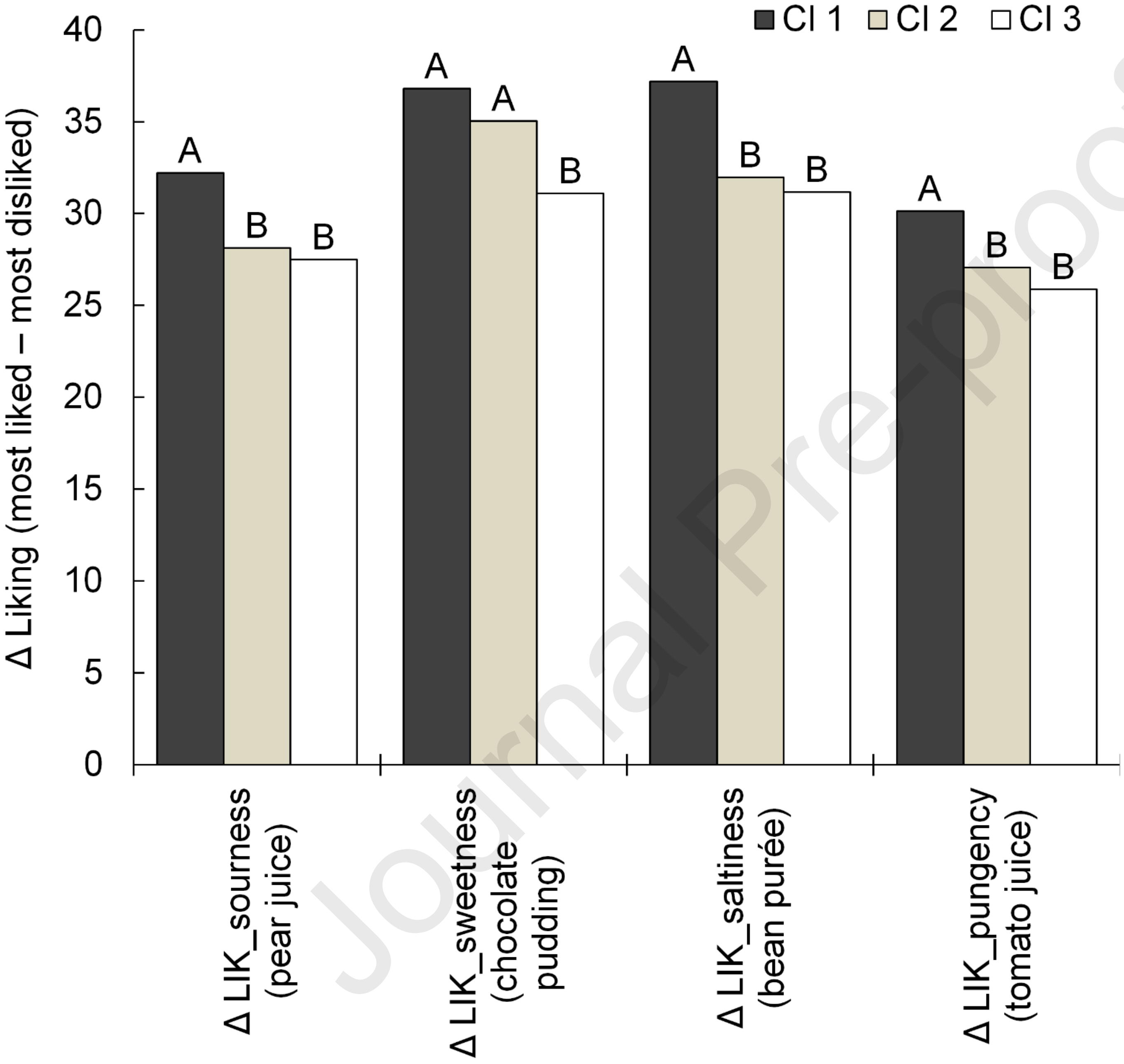
- Subjects highly responsive to basic tastes are also highly responsive to astringency, pungency, PROP
- Oral responsiveness is related to responsiveness to odorants with trigeminal activity
- Oral irritation (capsaicin) and nasal irritation (odorants with chemesthetic activity) are correlated
- Hyper-responsive subjects have a higher hedonic variation (span in liking ratings)
- Less responsive subjects require greater modifications in products to modify their liking


Bitter_index
Sour_index
Umami_Index
Salty_Index
Sweet_index
PC2 (12.5 %)
PC1 (60.0 %)
4
3
2
1
0
-1
-2
-3
-4
-4
-3
-2
-1
0
1
2
3
4



Umami_Index
Salty_Index
Bitter_Index
Sweet_Index
Sour_Index
PC3 (11.0 %)
PC4 (9.3 %)
5
4
3
2
1
0
-1
-2
-3
-4
-5
-5
-4
-3
-2
-1
0
1
2
3
4
5


Cl 1
Cl 2
Cl 3
0,40
0,30
0,20
0,10
0,00
-0,10
-0,20
-0,30
-0,40
Δ INT std (C4-C1)
A
B
B
A
B
C
A
B
B
A
AB
B
Δ INT_sour (pear juice)
Δ INT_sweet (chocolate pudding)
Δ INT_salty (bean purée)
Δ INT_pungency (tomato juice)


Cl 1
Cl 2
Cl 3
Δ Liking (most liked – most disliked)
0
5
10
15
20
25
30
35
40
A
B
B
A
A
B
A
B
B
A
B
B
Δ LIK_sourness (pear juice)
Δ LIK_sweetness (chocolate pudding)
Δ LIK_saltiness (bean purée)
Δ LIK_pungency (tomato juice)