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Two decades of supertasting: where do we stand?

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Abstract

Oral chemosensation can vary greatly across individuals, both in terms of the lowest concentration that can be detected (threshold) and in the magnitude of perceived intensity for stimuli at higher concentrations (suprathreshold response). Individuals who experience greater taste intensity are often termed supertasters, and this phenotype has typically been measured via the suprathreshold bitterness of the tastant propylthiouracil (PROP). Notably, supertasting extends beyond bitterness and other tastants to include oral somatosensation and retronasal olfaction, and it may also include finer acuity as well. Here, we describe the evolution of the supertasting concept over the last 20 years, and summarize the current state of the field. Alternative phenotyping approaches that not dependent on PROP are reviewed, and the molecular genetics of broadly tuned heightened taste and orosensory response are discussed. We conclude by initiating a conversation on nomenclature as we look toward the next 20 years of chemosensory research.

1. Introduction

Taste is a sentinel of the alimentary tract, preventing the ingestion of toxins and informing the ingestion of nutrients. Given this sentinel function, the evolutionary mechanism behind variation in taste is less clear, although it presumably confers some advantage given the parallel, independent evolution of dimorphic taste phenotypes in human and non-human primates [1]. Reports that humans vary in taste ability date back to 1888 [2]; the next major advance occurred in 1931 with the dual discovery of ‘taste-blindness’ for thiourea compounds [3] and the heritable basis for this trait [4]. Over the next 80 years, differences in detection thresholds were eventually studied hundreds of times across thousands of participants (see [1]). In 2003, allelic variation in the bitter receptor gene *TAS2R38* was implicated as the molecular basis of differences in phenylthiocarbamide (PTC) detection thresholds [5], and quickly extended to include propylthiouracil [6].

However, over the past two decades, the study of individual differences in oral sensation has also grown to include the idea of supertasting. Originally identified as the heightened response to the suprathreshold bitterness of concentrated propylthiouracil (PROP) [7], the contemporary view supports that supertasting encompasses elevated response to all taste qualities (e.g., [8, 9]), as well as oral somatosensation [10, 11] and even retronasal olfaction

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[12]. Examination of molecular genetics in this context indicate *TAS2R38* alleles cannot explain supertasting [9]. This makes intuitive sense, as it is hard to envision how polymorphisms in a narrowly tuned bitter receptor gene could mechanistically explain elevated response across multiple taste qualities, oral somatosensation and retronasal olfaction. Thus, present work by Calò and colleagues [13] represents a promising step forward for the field as the identification of a novel polymorphism that may explain variation in suprathreshold response more broadly is of critical interest. The research by Calò et al was restricted to propylthiouracil bitterness – it remains to be determined whether this SNP associates with heightened response to other stimuli or with taste papillae or taste bud density.

2. Two distinct phenotypes for bitterness

PROP supertasters are identified by perceived intensity [7] and *not* by threshold measures [14]. That is, detection threshold and suprathreshold response (perceived bitterness) are two related but distinct phenotypes [9, 15]. This is a critical distinction, because direct scaling (see [16, 17]) provides a means to measure a range of perceptions that cannot be quantified with threshold tasks based on signal detection theory. This is especially critical for chemosensory response as it relates to ingestive behavior and health, as threshold and suprathreshold response can be decoupled, both across compounds and individuals [15, 18]. As an example, threshold does not predict intake of salt or alcohol while suprathreshold measures do [19-21].

3. Origins of the Term Supertaster

The term supertaster first appeared in print in a 1991 article by Linda Bartoshuk in the trade journal *Food Technology*. In her laboratory, Bartoshuk and colleagues had noticed non-tasters were relatively homogeneous in response, while the tasters were much more variable, including a subgroup who found PROP to be intensely bitter. They called those people 'supertasters'. This observation was presaged by a rarely cited 1979 report showing a subset of PTC tasters gave high intensity ratings for the bitterness of creatinine and quinine, suggesting a general response difference, as these stimuli act via different mechanisms [22]. In the seminal data paper on supertasting [7], supertasters were identified by the ratio of the perceived intensity of PROP to the perceived intensity of sodium chloride. Similar approaches based on graphical rather mathematical methods are also common (eg, [23]). However, subsequent work indicates supertasters also perceive salt more intensely when using a non-taste cross modal standard [20, 24]. This makes salt-based classification methods less than ideal from one perspective, as misclassification bias may cause effect sizes to be underestimated. Thus, many contemporary reports each use the PROP bitterness rating with *a priori* cutoffs (eg, [20]), or use a non-taste reference such as the brightness of the sun (eg, [25]) or sound (eg, [19]). Alternatively, salt-based methods are inherently conservative, which may appeal to some researchers. The present work by Calò and colleagues uses a salt based method to classify individuals trichotomously as non-, medium, and supertasters, which suggests effect sizes in future replications could be even larger.

4. Greater acuity in supertasters

Two converging lines of evidence, one direct and one indirect, suggest supertasting may not be limited to greater orosensory response but may also include greater chemosensory acuity. In particular, supertasters have smaller average Weber fractions for model foods [26]. That is, supertasters are able to discriminate smaller changes in ingredient levels in a forced choice task paradigm, which is consistent with other reports based on suprathreshold methods [11, 20]. The greater acuity hypothesis is indirectly supported by evidence that wine experts (Hayes & Pickering, under review), chefs [27] and 'foodies' (individuals who

give higher affective ratings to food than nonfood items) [28] are more likely to be supertasters.

Notably, the relationship between intensity, liking/rejection and supertasting appears to vary across foods and taste qualities. For some, more intense sensations lead to disliking (eg, fat/sugar mixtures; [29]) while for others, liking increases with intensity without any apparent asymptote (eg salty snacks; [21]). Therefore supertasters reach an optimal concentration more quickly in the first case, but not the second. Thus, while the concentration intensity function is steeper for supertasters, different psychohedonic functions for specific foods or tastes make it difficult to form sweeping generalizations regarding supertasting and liking. For example, the increased bitterness may be protective against alcohol intake in some individuals [30], while finer acuity may be advantageous for those for those who overcome the initial aversion and learn to like alcoholic beverages (Hayes & Pickering, under review).

5. Moving Beyond Prop

Although supertasting and PROP bitterness have been largely synonymous (and contentious) for the last two decades, one can gain important insight by carefully distinguishing between the construct of supertasting – heightened orosensory response that is broadly tuned – and its historical operationalism via PROP [9]. Indeed, two non-PROP based measures for identifying individuals with heightened taste response have been reported previously [8, 31]. The first, irritant bitter tasting (iBT), is based on the observation that approximately half of individuals tested report a bitter side taste from the prototypical irritants capsaicin, piperine, and zingerone on the posterior tongue [31-33]; these individuals also report greater sweetness, sourness, saltiness, and bitterness from the prototypical tastants sucrose, citric acid, salt, and quinine [31]. Nor is this limited to the posterior tongue: reanalysis of data from [32] indicates iBTs also report greater taste intensity on the anterior tongue. The second non-PROP method for identifying supertasting-like phenomena is thermal tasting (TT). Some individuals report taste phantoms when small regions of the tongue are heated or cooled in a specific temporal pattern [34]; these individuals also report greater perceived intensity, both with regional and whole mouth taste stimulation, and even retronasal odorants [35]. Unfortunately, both of these methods result in a large minority of individuals being unclassifiable, either due to inability to visualize the circumvallate papillae [31] or intermittent response to thermal stimulation across trials [8]. Additionally, in contrast with PROP, neither of these phenotyping methods have been adapted to field use yet. Moreover, all phenotyping methods are difficult to execute well, and expensive in terms of time and labor. If future work indicates that the gustin polymorphism identified by Calò et al can act as a *genotypic* marker for supertasting, this would represent a major advance in our ability to study chemosensory influences on dietary behavior at an epidemiological level. Of course, behavioral (ie, phenotypic) measures are still highly desirable if at all possible, as a genotype may become decoupled from the observed phenotype due to environmental exposure, as occurs with taste nerve damage [19, 36]. Thus, one single marker, be it phenotypic or genotypic, is insufficient to fully characterize orosensory response as it relates to diet and health and multiple markers are needed (see [37, 38]).

6. Supertasting – The Future?

PROP bitterness and the jargon supertasting are so thoroughly enmeshed in both the scientific literature and the public consciousness, that attempting to disentangle them seems nearly impossible. However, elevated responses of TTs and iBTs are independent of PROP bitterness [8, 32], and this raises an important semantic issue: is it appropriate to consider these individuals supertasters? Secondly, is it possible to be a general supertaster (gST; [39]) while not being a PROP supertaster (pST)? Lim and colleagues have suggested

variance in overall taste response may be captured better by other prototypical tastants instead of PROP [40]. Finally, with better understanding of the genetics of bitter taste perception, we now understand that individuals may have elevated response to specific bitter tastants independently of others, as shown genetically [41, 42] and psychophysically [15, 43]. Thus, is it reasonable to speak of ‘genetic supertasters’ (eg PAV/PAV homozygotes, who may not actually be PROP supertasters phenotypically) or ‘generalized supertasters’ (those who have elevated response to sucrose and quinine but not PROP)? Is it appropriate to describe someone as a ‘saccharin supertaster’ or a ‘grapefruit supertaster’? It seems all of these potentially dilute the original meaning sufficiently to make it useless. Also, as we learn more about differences in the perception of umami [44] and sweet tastes [45], we risk being buried under an alphabet soup of prefixes (pST, gST, uST, sST, etc).

Given the totality of evidence and arguments presented here, we suggest now is the appropriate time to begin to clarify the terminology we use, as a field, to describe broad, elevated chemosensory response across stimuli. Thus, we would like to suggest that a new phase should be adopted for broadly tuned heightened taste response. One potential candidate would be hyperguesia. The Greek roots and intended meaning are readily apparent to practitioners in the field, it has minimal prior usage in the literature (3 English language hits in PubMed), and it is free of the near synonymous association with propylthiouracil.

We all owe a strong debt of gratitude to pioneers in taste research, specifically those working on the genetics of thiourea compounds as they provided a valuable framework to study chemosensation, diet and associations with health. Looking forward, it is apparent that oral chemoreception research is evolving to encompass alternate paradigms that include a functional oral nutrient detection system [46, 47], independent of the perception of prototypical tastes and somatosensory and chemesthetic qualities. The last two decades of research in chemosensation have been hard fought – looking forward, the field should now move beyond our focus on thiourea genetics to consider the role of chemosensory variation in dietary behavior, and health and wellness more broadly [37, 42, 44].

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