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Thermal taster status: A review of physiological aspects, methodological variables in phenotypical characterisation and relationship with sensory perception and affective response

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ABSTRACT

Thermal taster status (TTS), the ability to perceive tastes from lingual thermal stimulation, is a phenotype first observed in 2000. Due to limited data available, knowledge on this phenotype is still scarce. This review assessed existing literature (from 2000 to 2025) on TTS considering physiological aspects; methodological variables related to the determination of TTS and participant classification; socio-demographic factors and other orosensory phenotypes; the relationship between TTS and consumer affective responses to food and beverage. It showed that TTS represents a source of individual taste variation that discriminates between thermal tasters and thermal non-tasters, where the former are found to be more responsive to taste and chemesthetic sensations, in watery solutions, beverages and liquids. Despite only a few studies evaluating the effect of TTS on food and beverage sensory perception, it emerged that TTS could have an influence on food liking. However, several limitations in this field of research were identified and future research perspectives are suggested. This review contributes to understanding how this taste phenotype may play a key role in food preferences, food intake, and diet-related diseases. A deeper understanding of the impact of TTS on sensory perception through future research is warranted.

1. Introduction

The perceived intensity of taste and other oral sensations vary considerably among individuals and is a primary factor influencing food choices, likely affecting nutrition status, body weight, and overall health (Nolden & Feeney, 2020; Yang et al., 2020). Food choice and preference may also have different origins, including governmental and media political influences, environmental, socio-cultural or purely individual factors, such as demographic, physiological, psychological, genetic, and behavioural (Monterrosa et al., 2020). Generally speaking, oral responsiveness may affect the hedonic response toward food and beverages in opposite directions, depending on whether the elicited sensations are perceived as pleasant or aversive. An extended literature review shows that highly oral-sensitive participants may limit or avoid food matrices (e.g. fruits and vegetable, alcohol) that elicit orosensations that are generally considered aversive (e.g. bitterness, sourness, astringency, pungency) resulting in limiting/avoidance of certain foods (Bell & Tepper, 2006; Dinnella et al., 2011; Pagliarini et al., 2021). It has also been hypothesised that these individuals experience greater reward from pleasant taste sensations during eating (e.g., sweetness), which may lead to increased consumption of highly palatable foods (Armitage et al., 2021; Thibodeau & Pickering, 2019). Thus, responsiveness/sensitivity to the sensations characterising food may contribute to an unbalance in food intake. Individuals who are overweight or obese show reduced oral responsiveness compared to normal weight individuals (G. Li et al., 2023; Proserpio et al., 2016). Recent evidence suggests that some individuals exhibit higher orosensory responsiveness across multiple modalities, leading to heightened hedonic discrimination in response to subtle variations in food composition (Piochi et al., 2021a).

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Beyond inter-individual differences in overall oral responsiveness, multiple taste phenotypes have been described—including PROP supertaster status (Dinnella et al., 2011; Piochi et al., 2021a; Tepper et al., 2017), sweet-liking phenotypes (Yang et al., 2019), fatty-acid (fat) taste sensitivity (Prinz et al., 2007), —each linked to variability in taste intensity perception and food liking. One of the most recent phenotypes discovered, which may contribute to food preferences, is 'thermal taster status' (TTS), first reported by Green (2021) whereby a thermally induced taste sensation (thermal taste) can be elicited when the tongue is thermally stimulated in the absence of a taste stimulus. Those who report a taste when the tongue is thermally stimulated (warmed and/or cooled) using a thermode placed on the tongue are called thermal tasters (TTs) (Bajec & Pickering, 2008; Green & George, 2004). During thermal elicitation, TTs perceive prototypical tastes (sweet, bitter, umami, salt, and sour) or other oral sensations (minty, metallic, spicy), with the reported sensations varying with the temperature regime of warming or cooling and from individual to individual (Bajec & Pickering, 2008; Green, 2021; Hort et al., 2016; Skinner et al., 2018; Yang et al., 2014). On the other hand, those who only report a change in temperature are classified as thermal non-tasters (TnTs). Since the discovery of TTS, a series of investigations have studied the responses of TTs and TnTs during thermal stimulation and to aqueous solutions, foods and beverages when tasting them.

Early studies defined thermal taste as a "phantom taste," emphasizing that a taste-like sensation was reported without a chemosensory stimulus (e.g., Cruz & Green, 2000). However, the stimulus is known to be temperature, based on converging psychophysical evidence and plausible peripheral mechanisms —e.g., lactisol blockade of TAS1R2/TAS1R3 abolishing thermal sweetness and the heat-sensitivity of TRPM5 implicated in sweet/bitter/umami signalling (Nachtigal & Green, 2020; Talavera et al., 2005, 2007). For this reason, the terms "thermal taste" or "thermally induced taste" have been adopted. The operational definition of TTs as a phenotype or group has also expanded along four axes: temperature window, taste categories included, minimum intensity required, and replicability requirements. These variations in definition help to explain differences between studies in prevalence estimates, and the emergence of an unclassified group.

This review aimed to summarise the available literature on TTS and identify gaps in our current understanding of the phenomenon. In particular, the physiological mechanisms identified so far that may regulate TTS were analysed; the effect of TTS on orosensory responsiveness was explored; methodological aspects related to the determination of TTS were also considered, including variations between the methods used and unresolved aspects; the relationship between the TTS and socio-demographic characteristics of participants and possible relationships with other taste phenotypes. Finally, research investigating TTS's potential effect on food perceptions and preferences was evaluated.

2. Methodology

A literature review was conducted to outline and map all scientific advances made on the topic of TTS from the first scientific publication to the present.

This review was carried out following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) scheme, ensuring

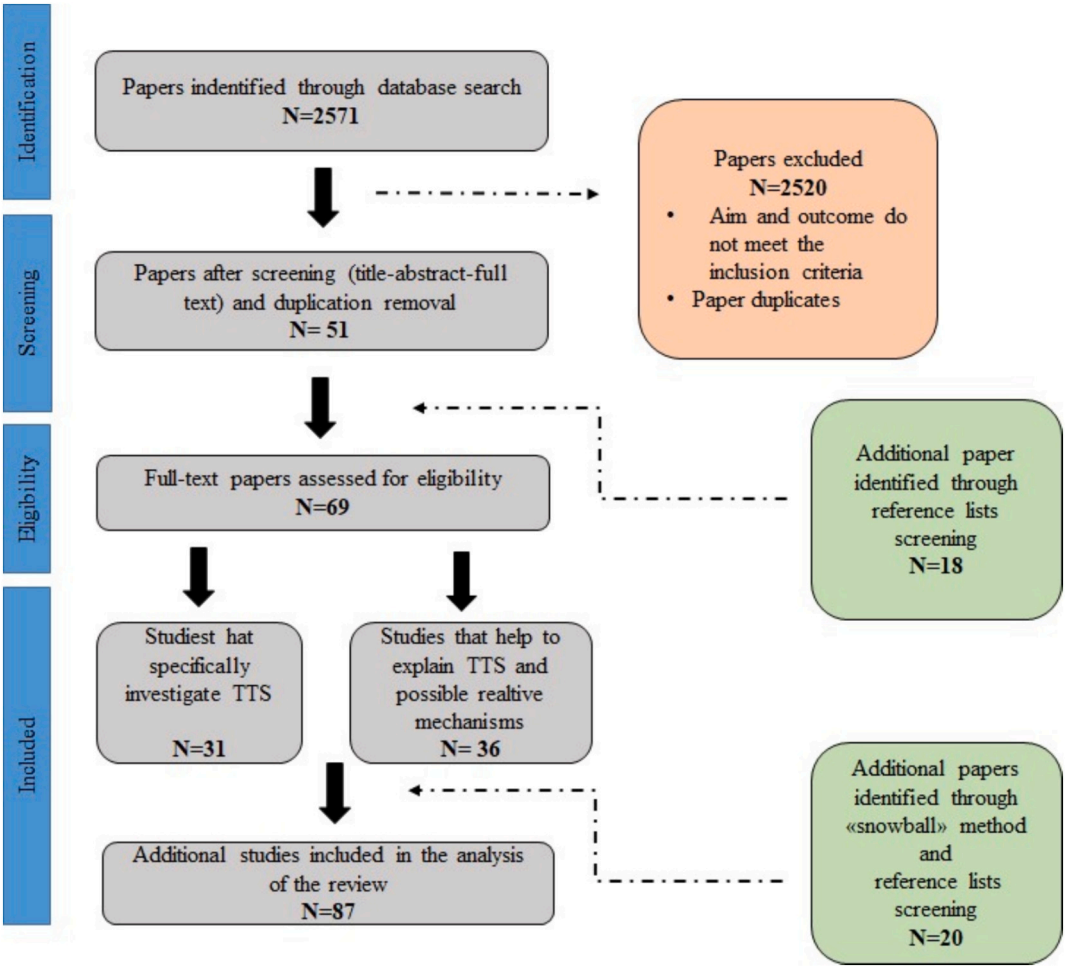

Fig. 1. Applied methodology for the systematic review and meta-analyses (PRISMA and "snowball" method).

transparency and robustness of the review (Fig. 1). To identify articles, a search was conducted using Scopus and Web of Science as the database (https://www.scopus.com/). The search was limited to include studies published between 2000 and 2025.

The following combinations of search strings were used for item selection:

- thermal AND taste;
- thermal AND taste AND status;
- thermal AND taster AND status;
- thermal AND taster AND status AND food AND liking;
- thermal AND taster AND status AND orosensory;
- thermal AND taster AND status AND PROP;
- thermal AND taster AND status AND mechanism;
- thermal AND taster AND status AND genetic;
- thermal AND taster AND status AND cortical AND response;
- thermal AND taster AND status AND trigeminal AND taste;
- thermal AND taster AND status AND food AND behaviour;
- thermal AND taster AND status AND gender;
- thermal AND taster AND status AND age;
- thermal AND taster AND status AND ethnicity.

Scopus and Web of Science databases search generated 2571 published in English.

To be eligible for inclusion, papers had to include references to TTS, information that could describe and explain this taste phenotype from any point of view, and analyse any relationships with other phenomena. After title/abstract/full-text screening and removal of duplicates, 51 records remained.

To ensure completeness, backwards and forwards citation tracking was performed, leading to the inclusion of an additional 18 relevant articles. These relevant articles, which used broader or related terminology, were only retrieved during citation linking, since the initial search focused on specific terms related to TTS. This resulted in a final set of 69 papers included in the review. Among the included publications, 31 specifically investigated TTS, whilst 36 were used to explore related mechanisms, including peripheral and central pathways, chemosensory physiology, and individual variability in sensory perception.

In addition, the documents were also analysed using the "snowball" method, a non-probabilistic sampling technique, to complete the final sample (Lecy & Beatty, 2012). Specifically, the list of document references or citations was used to identify other documents. Documents published by the cited sources, such as additional material found through the snowball approach, were skimmed for information that could aid the review and were otherwise excluded from the analysis, reaching a total of 87 documents.

A thematic mapping of these 31 papers was performed to identify and visualize the key research areas explored in the literature to date (Fig. 2) and characterised according to the journals in which they were published (Table 1–26 article +5 PhD thesis)).

3. Methodological aspects in thermal stimulation

3.1. Procedure to determine TTS: main variants

The determination of TTS has traditionally followed the original procedure outlined by Bajec and Pickering (2008), widely adopted in subsequent studies (Bajec, 2011; Bajec et al., 2012; Bajec & Pickering, 2010; Bering et al., 2014; Pickering, Bartolini, et al., 2010; Pickering, Moyes, et al., 2010; Pickering & Klodnicki, 2016; Pickering & Kvas, 2016; Eldeghaidy et al., 2018; Mitchell et al., 2019; Pickering et al., 2016; Small-Kelly, 2018; Small-Kelly & Pickering, 2020; Thibodeau et al., 2019, 2020; Pickering & Pickering, 2022; Thibodeau & Pickering, 2021). This method uses a thermode consisting of a 64-mm^2 Peltier device with thermocouple feedback applied at three locations on the anterior tongue: the tip, 1 cm to the left, and 1 cm to the right of the midline. By contrast, several protocols employed larger, single-site thermodes that stimulate a wider anterior-tongue patch in one placement (e.g., 256 mm^2 square ATS - advanced thermal stimulator: Eldeghaidy et al., 2018; Skinner et al., 2018), thereby stimulating a similar area as the smaller probes in a single placement. Since the tongue tip is

Table 1
Outlets for publications of reviewed TTS publications and impact factor of the reviewed publications ($N = 27$).

Journal	Impact Factor	Number of publications
Physiology and Behaviour	2.4	7
Food Quality and Preference	4.9	6
Chemosensory Perception	0.8	6
Chemical Senses	2.8	2
Journal of the Institute of Brewing	–	1
Australian Journal of Grape and Wine Research	2.5 (2023)	1
Flavour	Flavour ceased to be published by BioMed Central in 2017	1
Beverages	3	1
Human Brain Mapping	3.5 (2023)	1
Nature	50.5	1

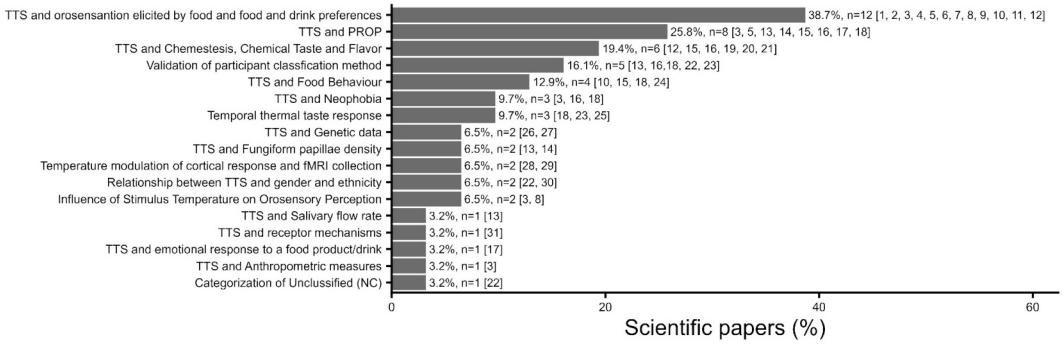

Fig. 2. Mapping of the research objectives pursued from 2000 to the present on Thermal Taster status. [1] Bajec, 2011; [2] Bajec et al., 2012; [3] Bajec & Pickering, 2010; [4] Pickering, Bartolini, et al., 2010; [5] Pickering, Moyes, et al., 2010; [6] Pickering & Klodnicki, 2016; [7] Pickering & Kvas, 2016; [8] Mitchell et al., 2019; [9] Pickering et al., 2016; [10] Small-Kelly, 2018; [11] Small-Kelly & Pickering, 2020; [12] Thibodeau & Pickering, 2021; [13] Bajec & Pickering; [14] Eldeghaidy et al., 2018; [15] Yang, 2015; [16] Thibodeau et al., 2019; [17] Yang et al., 2018; [18] Botha, 2024; [19] Green et al., 2005; [20] Green & George, 2004; [21] Yang et al., 2014; [22] Thibodeau et al., 2020; [23] Botha et al., 2021; [24] Pickering & Pickering, 2022; [25] Skinner et al., 2018; [26] Bering, 2013; [27] Bering et al., 2014; [28] Eldeghaidy et al., 2021; [29] Hort et al., 2016; [30] Yang et al., 2020; [31] Nachtigal & Green, 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

particularly responsive to thermal stimuli, likely due to its dense innervation by fungiform papillae (Cruz & Green, 2000; Piochi et al., 2018; Shahbake et al., 2005), other studies instead used smaller circular ATS tips (~28.26 mm^2), prioritising spatial specificity over coverage (Eldeghaidy et al., 2018, 2021; Hort et al., 2016; Yang et al., 2014, 2018, 2020). These devices are commercially available and widely reported in the literature. Fig. 3 schematically illustrates the probe geometry, contact positions on the tongue (anterior tip and lateral regions), and the application method in the most commonly used protocol, adopted by Bajec and Pickering (2008) and in many subsequent studies.

Previous studies used more moderate temperature ramps (15–35/35–15 °C; Green & George, 2004; Green et al., 2005), while subsequent works largely adopted the procedure described below. In particular, the standard procedure includes warming and cooling cycles conducted in sequence and replicated twice. Warming trials start at 35 °C, cool to 15 °C, and re-warm to 40 °C for 1 s. Cooling trials begin at 35 °C, cool to 5 °C, and hold for 10 s, with temperature changes occuring at 1 °C/s in both directions. Although two replicates are typical, some protocols introduce an adjudication replicate when taste quality or presence is inconsistent across runs (Skinner et al., 2018). Participants rate sensations using generalised labelled magnitude scales (gLMS) (Bartoshuk et al., 2004), assessing respectively the intensity of "temperature", "sweet", "salty", "sour", "bitter", and "other sensations" to capture any other oral sensations that might be experienced during thermal stimulation. Later studies included additional categories such as "umami" and "metallic" among thermally elicited tastes (Thibodeau et al., 2019, 2020). These expansions highlight evolving classification frameworks aimed at capturing a broader range of sensations.

A persistent challenge concerns participant classification, which varies across studies and is rooted in the procedural/operational differences catalogued in Table 2. Participant classification varies widely across studies, driving large differences in reported TT prevalence (≈21–50 %; Bajec & Pickering, 2008; Cruz & Green, 2000) and a sizeable Not classified (NC) groups (≈21–60 %; Skinner et al., 2018; Thibodeau et al., 2019). This variability stems from (i) three-site rather than single-site protocols, which increase site−/regimen-specific inconsistencies; (ii) heterogeneous operational rules (e.g., 'above weak' with same taste/site reproducibility; requiring responses in both warming and/or cooling; or no minimum intensity); (iii) differences in scaling/anchors and response options (inclusion of "umami/metallic") and (iv) differences in the demand characteristics on participants when reporting thermally elicited sensations (e.g., CATA vs intensity ratings, yes/no or rating of all scales). In this context, demand characteristics—features of an experimental method that may unintentionally bias participant responses—are a key consideration in TTS research. Simply screening for TTS may imply that participants are expected to experience a taste during thermal stimulation. Although participants are informed that all responses are valid (Bajec & Pickering, 2008; Green & George, 2004), early studies adopted a "weak" threshold to minimise response bias and ensure that only valid TTs were identified. Similarly, the NC group was introduced to ensure that only true TnTs were classified as such (Bajec & Pickering, 2008). Nevertheless, these classification rules, together with the demand characteristics of TTS screening, likely contributed to the misclassification of TTs and TnTs as NC. Thus, the diversity of methodologies across studies reflects the field's developmental trajectory, where stricter screening protocols were initially necessary to establish the legitimacy of thermally elicited taste sensations and have been progressively relaxed in response to growing empirical evidence. As understanding of TTS advances, efforts are increasingly focused on refining screening approaches and establishing best practices. Taken together, these procedural differences and demand characteristics shape what counts as a valid thermally elicited taste and hence TT/TnT/NC assignment, and the large NC proportions complicate cross-study comparisons and mechanistic inference. The Rapid Combined Phenotyping for Thermal Taste (RapCoTT) method was shown to align closely with traditional methods, emphasizing its potential for efficient large-scale studies (Botha et al., 2021). The combined temperature regime combines the warming and cooling cycles into a single cycle, reducing the number of trials needed. Furthermore, the use of TCATA allows participants to provide responses in real time, reducing the cognitive burden on participants during screening, and avoiding working memory interference effects. In addition, the precise timing of thermal taste onset and offset enables a more thorough investigation of thermal taste mechanisms and grouping of thermal tasters (Botha, 2024). These methodological innovations require continuous validation across different groups of participants, varying in age, gender, language/culture, and taste perception, to ensure consistency and reliability.

3.2. *Unsolved methodological aspects*

Early studies classified TTs based on a taste response above "weak" on the gLMS scale in duplicate trials, which yielded a TT prevalence of approximately 50 % (Cruz & Green, 2000). This method was refined by incorporating an additional category for NCs, identifying those who did not consistently report a taste response, leading to a lower TT prevalence of 20 % and classification of 40 % of participants as TnTs (Bajec & Pickering, 2008). This classification framework was then applied consistently across subsequent studies from the same laboratory, whereas most methodological variation in the literature arose between laboratories. Later work identified 27 % of participants as TTs and 28 % as TnTs, defining TTs as those who reported any taste sensation above "weak," without requiring the same taste to be replicated across trials (Yang et al., 2014). Additional modifications considered participants as TTs if they reported any taste sensation above "weak" in both warming and/or cooling trials (Hort et al., 2016; Yang et al., 2018). Further changes allowed classification without specifying a minimum taste intensity, yielding 28 % TTs, 51 % TnTs, and only 2 % NCs (Skinner et al., 2018). The first study to focus on characterising unclassified participants

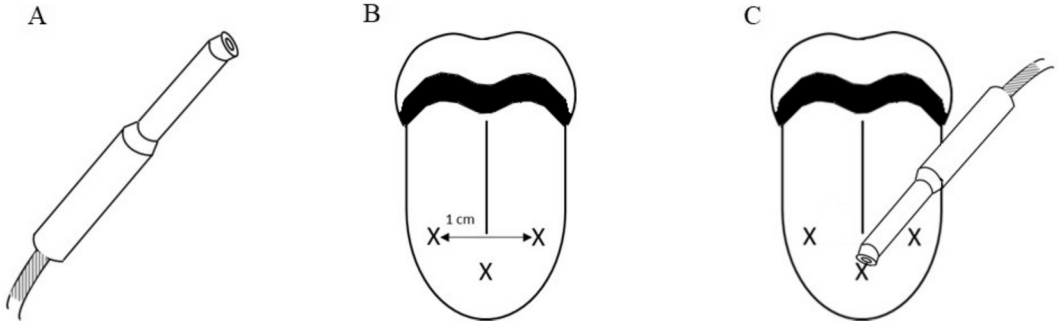

Fig. 3. Stylized representation of the thermode and its application to the anterior tongue: A) Stylized representation of the Peltier thermode used for Thermal Taster Status determination; B) Target sites on the anterior tongue (tip, and left/right lateral regions) typically used for Thermal Taster Status determination; C) Example of thermode application to each site during warming/cooling ramps.

Table 2
Methodological approaches used to determine the thermal taster status.

Temperature 1 °C/s	Position	Thermode characteristics	Repetitions	Training and evaluation scale	Classification	Classification summary (key requirements)	Reference
WC: 15 to 35 °C CC: 35 to 15 °C	**3 sites:** the edge of the tongue (the most anterior tip), and approximately 1 cm to the right and then the left of the midline	64 mm^2, Peltier thermoelectric module (shape not reported)	2	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who reported a taste that was at least 'weak' in intensity on the gLMS during either warming or cooling. It should be confirmed with a re-test. **TnT:** any participants not classified as a TT. **NC:** not included.	**Threshold:** ≥ "weak". **Replication**: taste in either WC or CC, confirmed on retest. **Same quality/site**: not required. **NC**: not used.	Green et al., 2005; Green & George, 2004
WC: 15 to 40 °C CC: 35 to 5 °C	**3 sites**: the edge of the tongue (the most anterior tip), and approximately 1 cm to the right and then the left of the midline	64 mm^2, Peltier device with a thermocouple feedback attached to a toothbrush sized water-circulated heat sink (square)	2	**Training:** - Early protocol: basic taste training using gLMS (and gVAS, where applicable), including repeated tasting and correct identification of all orosensations. Participants who failed this step were excluded. - Revised protocol: shortened familiarisation step without exclusion; Mitchell et al. (2019) also introduced "umami" and "metallic" as additional response options. **Evaluation:** gLMS (all studies); TCATA additionally used during screening in Mitchell et al. (2019).	**TTs**: who reported the same taste sensation, rated above weak on the gLMS, at the same location and temperature trial in both replicates. **TnT:** who did not perceive any taste sensation in any trial. **NC:** who is not classified as a TT or TnT.	**Threshold**: ≥ "weak". **Replication**: same quality at the same site and same trial across 2 replicates. **Regime**: WC or CC. **NC**: all non-conforming.	Bajec & Pickering, 2008 Bajec & Pickering, 2010 Bajec et al., 2012 Bering et al., 2014 Pickering, Bartolini, et al., 2010; Pickering, Moyes, et al., 2010 Pickering et al., 2016a, 2016b; Pickering & Klodnicki, 2016 Mitchell et al., 2019 Small-Kelly & Pickering, 2020 Pickering & Pickering, 2022 Thibodeau et al., 2020
WC: 15 to 40 °C CC: 35 to 5 °C	**1 site**: anterior tongue tip	256 mm^2 (square surface)	2	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who reported the same taste sensation, rated above weak on the gLMS, at the same location and temperature trial in both replicates. **TnT:** who did not perceive any taste sensation in any trial. **NC:** who is not classified as a TT or TnT.	**Threshold:** ≥ "weak". **Replication**: same quality at same site (single tip) and same trial across 2 replicates. **Regime**: WC or CC. **NC**: non-conforming.	Eldeghaidy et al., 2018
WC: 15 to 40 °C CC: 35 to 5 °C	**3 sites:** the edge of the tongue (the most anterior tip), and approximately 1 cm to the right and then the left of the midline	64-mm^2, computer-controlled Peltier device with a thermocouple feedback attached to a toothbrush-sized water-circulated heat sink (square)	2	**Training:** -gLMS -gVas **Evaluation:** gLMS	**TTs:** who reported taste sensations during both warming and cooling trials rated above 'weak' on the gLMS. **TnT:** who did not perceive any taste sensation in any of the temperature trials. **NC:** NC-AW subjects that had provided a minimum of one above weak thermal taste response.NC-BWO: provided ratings of below weak for both	**Threshold**: ≥ "weak". **Regime**: taste present in both WC and CC. **NC**: subdivided (AW/REP, AW/NoREP, BWO/REP, BWO/NoREP) by intensity/replicability.	Thibodeau et al., 2019

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Table 2 (*continued*)

Temperature 1 °C/s	Position	Thermode characteristics	Repetitions	Training and evaluation scale	Classification	Classification summary (key requirements)	Reference
					replicates. NC-REP: Same location and same taste. NC-NoREP: not consistent with responses		
WC: 15 to 40 °C CC: 35 to 5 °C	**1 site**: anterior tongue tip	28.26 mm^2, Peltier thermode, circular intra-oral ATS (advanced thermal stimulator) (truncated cone)	2	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who reported taste sensations during both warming and cooling trials rated above 'weak' on the gLMS. **TnT:** who did not perceive any taste sensation in any of the temperature trials. **NC:** people uncategorised due to inconsistencies in reporting taste sensations throughout the trials.	**Threshold:** ≥ "weak". **Regime**: taste required in both WC and CC. **Site**: tip (1 site). **NC:** inconsistent reporters.	Yang et al., 2014
WC: 15 to 40 °C CC: 35 to 5 °C	**1 site**: anterior tongue tip	28.26 mm^2, Peltier thermode, circular intra-oral ATS (advanced thermal stimulator) (truncated cone)	2	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who perceived a taste, above weak on the gLMS during both replicates of either the warming or cooling trial. **TnT:** who did not perceive a taste on any replicate of any trial. **NC**: not included.	**Threshold**: ≥ "weak". **Replication**: 2 replicates within the same regime. **Regime**: either WC or CC suffices. **NC**: not included.	Hort et al., 2016 Yang et al., 2018 Eldeghaidy et al., 2018 Eldeghaidy et al., 2021
WC: 15 to 40 °C CC: 35 to 5 °C	**1 site:** anterior tongue tip	256 mm^2, Peltier thermode intra-oral ATS (advanced thermal stimulator) (square surface)	3 (2 full, 1 as needed) If taste quality or taste presence were not consistent among replications, a third test was conducted to aid classification.	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who reported the same taste/s across two replicates of the warming and/or cooling trials at any intensity on the gLMS. **TnTs**: Those only perceiving temperature. **NC**: who reporder below weak are assigned to an uncategorised group; those reporting taste inconsistently (taste quality or the presence of taste) across ≥2 replicates were characterised uncategorised.	**Threshold:** none (any intensity). **Replication**: same quality across 2 replicates; adjudication 3rd replicate if needed. **Regime**: WC and/or CC. **NC**: < "weak" or inconsistent.	Skinner et al., 2018
WC: 15 to 40 °C CC: 35 to 5 °C	**1 site:** anterior tongue tip	Peltier thermode (Medoc, Israel) (advanced thermal stimulator) (circular)	2	**Training:** gLMS **Evaluation:** gLMS	**TTs:** who perceived a taste sensation from both replicates at either warming or cooling trials on the gLMS. **TnT:** who did not perceive any 'tastes' throughout the temperature trials. **NC**: individuals with inconsistent responses (e.g. only perceive taste from a single temperature trial), who were deemed the Uncategorised group.	**Threshold**: ≥ "weak". **Replication**: taste in both replicates within WC or CC. **NC**: single-trial or otherwise inconsistent responders.	Yang et al., 2020
Combined protocol 35 to 5 °C to 40 °C to 35 °C	**1 site:** anterior tongue tip	45 mm^2, Pelter device	2	**Training:** -gLMS -TCATA **Evaluation:** -gLMS -TCATA	**Scheme A** **TTs:** who reported any taste consistenly above weak on the gLMS in both initial replicates of	**Threshold**: ≥ "weak". **Replication**: consistent presence in 2 replicates of the same trial. **UC**:	Botha et al., 2021

(*continued on next page*)

Table 2 (*continued*)

Temperature 1 °C/s	Position	Thermode characteristics	Repetitions	Training and evaluation scale	Classification	Classification summary (key requirements)	Reference
					the same trial as TT **TnT:** who reported no tastes **UC (unclassified):** who reported taste in any trials but did not meet the classification criteria (either through consistency or intensity)	present but not meeting intensity/ consistency.	
					Scheme B **TTs:** who reported an expanded list of tastes regardless of intensity on any two replicates of the same trial as TT **TnT:** who reported no tastes **UC (unclassified):** who reported taste in any trials but did not meet the classification criteria (either through consistency or intensity)	**Threshold**: none. **Replication**: any listed taste on 2 replicates of the same trial. **UC**: presence/ consistency criteria not met.	
					Scheme C **TTs:** who reported an expanded list of tastes regardless of intensity on any two replicates of the same trial as TT using TCATA **TnT:** who reported no tastes **UC (unclassified):** who reported taste in any trials but did not meet the classification criteria (either through consistency or intensity)	**Threshold**: none. **Replication**: any listed taste on 2 replicates of the same trial. **UC**: presence/ consistency criteria not met.	

highlighted their potential relevance for understanding the mechanisms underlying thermal taste (Thibodeau et al., 2019). In particular, these participants were classified depending on taste intensity or taste and location reproducibility into four categories: 1) AW/REP – NC are those participants who provided at least one taste response above "weak" (AW) and one reproducible taste response during thermal stimulation (same taste, same position); 2) participants classified as AW/NoREP – NC were those providing at least one taste response above "weak" but no reproducible taste response during thermal stimulation; 3) BWO/REP – NC participants were defined as those who did not provide a gustatory response greater than "weak" ('below weak') but at least one reproducible gustatory response during thermal stimulation; 4) BWO/NoREP – NC participants who did not provide a gustatory response greater than "weak" or reproducible during thermal stimulation. It is possible that differences in the use of the gLMS scale between NCs and TTs, stemming from individual response strategies (e.g., conservative scale use) and from differences in training/familiarisation, complicates the use of "weak" as a universal cut-off for classification.

Building on this body of work, comprehensive mapping of reported experiences in a large TT sample (n = 254) tested whether thermally elicited qualities show a regional distribution across the tongue and temperature regimes, providing the most comprehensive mapping to date of associations among taste qualities, tongue sites, and warming/ cooling responses (Thibodeau et al., 2020). Specifically, distinct TT subgroups were identified based on (i) the predominant thermally evoked quality (sweet, salty, bitter, sour, umami, metallic, minty, spicy), (ii) the tongue location where it occurred, and (iii) whether it was elicited during warming or cooling. This subgroup structure supports the idea that multiple mechanisms underlie TTS. In terms of orosensory responsiveness to aqueous solutions no differences when tasting aqueous solutions of basic tastes were identified between any of the subgroups. This suggests that TTs can be treated as a homogeneous group when studying food-related behaviour. Nevertheless, more research is needed to confirm this hypothesis due to limitations in Thibodeau et al. (2020)'s work. In this same study, first, TTs were only included in the study if the thermally-elicited taste they reported was above 'weak' and reproducible. However, 41 % of participants in the study were classified as NC as the thermally elicited taste they experienced did not meet the strict criteria. Thus, it is plausible that differences in responsiveness would be found if the TT classification criteria had been relaxed. Second, intensity scores for the orosensations were converted to z-scores due to differences in methodology across the 12 cohorts of data that were combined (e.g., concentration, stimulus, Thibodeau et al., 2020).

Against this backdrop, an approach that assessed both heating and cooling within a single phenotyping protocol was first operationalised to aid classification (Skinner et al., 2018). Building on that precedent, Rapid Combined Phenotyping for Thermal Taste (RapCoTT method; Botha et al., 2021) integrates warming and cooling in one continuous sequence with real-time temporal check-all-that-apply (TCATA) reporting. In RapCoTT, classification relies on consistency rather than absolute intensity cut-offs: participants are classified as TT if they report

any listed taste on two replicates of the same trial; TnT if no tastes are reported; and NC only when tastes are reported but consistency criteria are not met. Applied within the same dataset, RapCoTT significantly reduces the number of NC identified (7 %) compared to traditional protocols (19–33 %), largely because it avoids reliance on an "above weak" cut-off and reduces working-memory and decision load by using a combined temperature regime (Botha, 2024; Botha et al., 2021). In this framework, participants report sensations immediately rather than retrospectively, which is expected to mitigate primacy (remembering mainly the first taste), recency (remembering mainly the most recent taste) and decay effects (loss of intensity with increasing working-memory load), and to limit potential confounding from the cooling phase of warming cycles. The higher engagement required by the task may also reduce intentional misreporting driven by experimental demand. In addition, RapCoTT shortens overall screening time because it does not require a gLMS training step and omits several extra procedures included in traditional protocols (Botha et al., 2021). In summary, RapCoTT offers a more standardised and efficient phenotyping workflow that improves classification yield without sacrificing comparability.

4. TTS status, thermally-elicited sensations and orosensory responsiveness

4.1. The sensations experienced during TTS screening

Table 3 shows the orosensations reported by TTs during thermal elicitation using the warming cycle, the cooling cycle, or through both warming and cooling cycles, from articles reporting the exact percentage. Not all TTs report the same experiences, these vary depending on the perceived orosensation, temperature range, and position tested on the tongue.

Thermally induced tastes/orosensations defined as valid for classification are: sweet, salty, sour, bitter, and umami/savoury, metallic, spicy (Botha et al., 2021; Skinner et al., 2018; Yang et al., 2014), tingling (Yang et al., 2014) and/or minty. Cooling cycles most commonly elicit bitter and sour thermal tastes, with saltiness also frequently reported during cooling (Cruz & Green, 2000; Pickering & Kvas, 2016; Skinner et al., 2018; Thibodeau et al., 2020; Yang et al., 2014; Yang et al., 2020). By contrast, sweetness is typically more prevalent during warming, although it can occur in both cycles (Cruz & Green, 2000; Pickering & Kvas, 2016; Skinner et al., 2018; Thibodeau et al., 2020; Yang et al., 2014, 2020). Other sensations observed during cooling include metallic, commonly reported with comparable frequency across warming and cooling (Botha, 2024; Botha et al., 2021; Skinner et al., 2018; Thibodeau

Table 3
Overview of the orosensations reported by thermal tasters (%) during thermal elicitation in warming cycle (WC), cooling cycle (CC) or accross both of them.

Subjects (n)	TTS (n)	Tongue response position	Sweet	Salty	Bitter	Sour	Umami/ savoury	Metallic	Minty	Spicy	Other	Reference
24	21 (one quality taste) 19 (two quality tastes)	Not specified	75 %	20.83 %		62.5 %						Cruz & Green, 2000
204	56	Tip	WC: 2 % CC: 8 %	WC: 3 % CC: 6 %	WC: 19 % CC: 26 %	WC: 10 % CC: 18 %	WC: 3 % CC: 1 %	WC: 30 % CC: 27 %			WC: 13 % CC: 14 % (including spicy and tingling)	Yang et al., 2014
44	23	Not specified	Both: 18 %	Both: 12 %	Both: 34 %	Both: 24 %					Both: 12 %	Pickering & Klodnicki, 2016*
44	25	Not specified	Both: 20 %	Both: 22 %	Both: 33 %	Both: 23 %					Both: 2 %	Pickering et al., 2016a)*
87	21	Not specified	WC: 27 % CC: 7 %	WC: 6 % CC: 27 %	WC: 33 % CC: 30 %	WC: 17 CC: 33					WC: 17 % (cinnamon n = 1; metallic *n* = 1; spicy/hot n = 1) CC: 3 % (spicy/hot n = 1)	Pickering & Kvas, 2016*
85	36	Tip	WC: 42 % CC: 7 %	WC: 5 % CC: 5 %	WC: 11 % CC: 25 %	WC: 8 % CC: 25 %		WC: 13 % CC: 17 %	WC: 8 % CC: 13 %	WC: 13 % CC: 8 %		Skinner et al., 2018
781	254	Location All 22 % Tip 23 % Right 14 % Left 13 % Tip & Right 8 % Tip & Left 9 % Left & Right 11 %	Both: 19 % WC: 28 % CC: 8 %	Both: 12 % WC:11 % CC:14 %	Both: 26 % WC: 25 % CC: 27 %	Both: 21 % WC: 10 % CC: 31 %	Both: 3 % WC: 4 % CC: 2 %	Both: 13 % WC: 12 % CC: 14 %	Both: 1 % WC: 0 % CC: 1 %	Both: 6 % WC: 10 % CC: 2 %		Thibodeau et al., 2020
24	12	Not specified	WC: 29 % CC: 16 %	WC: 7 % CC: 6 %	WC: 25 % CC: 23 %	WC: 18 % CC: 39 %		WC: 21 % CC: 16 %				Eldeghaidy et al., 2021

* Data from these studies was included in the analysis of Thibodeau et al., 2020 (Cohorts 4, 8 and 9).

et al., 2020; Yang et al., 2014, 2020). Consistent with this, some cohorts report comparable occurrences of metallic and bitter sensations across warming and cooling, which may partly reflect the temperature regimen—e.g., brief cooling phases within warming trials (Pickering & Kvas, 2016; Skinner et al., 2018; Thibodeau et al., 2020; Yang et al., 2014, 2020). The classification of spicy and minty sensations as thermally induced responses has been debated because these terms usually denote chemesthetic (trigeminal) qualities—burning/tingling for 'spicy' and cooling for 'minty'—classically induced by capsaicin and menthol. During TTS screening, however, analogous sensations can be reported under thermal stimulation alone, some protocols included 'spicy/minty' as valid thermally elicited sensations (Hort et al., 2016; Skinner et al., 2018; Yang et al., 2014), whereas others excluded them, arguing they likely reflect somatosensory/chemesthetic rather than gustatory processing (Thibodeau et al., 2019, 2020).

TTS determination should consider both direction of stimulation (warming vs cooling) and the specific taste identity when evaluating TTS. Sweet thermal taste was elicited during both warming (23–36 °C) and cooling (34–21 °C) phases (Botha, 2024); a warming-evoked sweet activation window of 22–38 °C is consistent with the thermosensitivity of TRPM5 (Skinner et al., 2018). Savoury taste was predominantly reported during warming in the 20–39 °C range, with a peak around 28 °C. Bitter and sour thermal tastes were mainly evoked during cooling, with activation peaks near 16–18 °C. Salty taste was also primarily elicited during cooling (24–17 °C), but additional response peaks were observed at 7 °C and again during warming between 27 and 33 °C (Botha, 2024).

Complementing these temperature ranges, model-based clustering of RapCoTT data identified three distinct thermal taste response clusters: (1) a metallic/salty cluster, occurring mainly during cooling; (2) an umami/acidic cluster, more frequently elicited during warming; and (3) a sweet/bitter cluster, with sweet responses often related to warming and bitter sensations to cooling (Botha, 2024). These clusters suggest the existence of at least three distinct subgroups within the TT phenotype, each characterised by specific taste–temperature profiles. Whilst a few participants exhibited mixed response patterns, the majority showed a clear tendency toward one cluster, allowing for their systematic classification and facilitating follow-up studies. For aqueous basic tastes, no systematic differences in orosensory reactivity emerged across cluster-defined TT subgroups (Botha, 2024); similarly, in work using an intensity-threshold approach without clustering, no systematic differences were found (Thibodeau et al., 2020).

4.2. Responsiveness to taste/chemesthetic stimuli and to temperature changes across different TTS phenotypes'

Studies consistently indicate that TTs perceive orosensations with greater intensity than TnTs. Research has shown that TTs rate the intensity of suprathreshold aqueous solutions of prototypical taste substances (sweet, sour, salty, bitter, umami) higher than TnTs, even across multiple taste sites, specifically the anterior tip and the two lateral anterior (right and left) tongue sites used in standard protocols (Bajec et al., 2012; Green et al., 2005; Green & George, 2004; Hort et al., 2016; Small-Kelly & Pickering, 2020; Thibodeau et al., 2019,2021; Yang et al., 2014). By contrast, the relationship between TTs and taste thresholds, as well as trigeminal stimuli, remains less clear. For example, higher detection threshold for NaCl and caffeine, but not for saccharose, have been reported for TTs, whilst detection thresholds for trigeminal stimuli (N-ethyl-2-isopropyl-5-methylcyclohexanecarboxamide and capsaicin) did not differ based on TTS classification (Yang et al., 2014). In general, TTs demonstrated greater sensitivity to complex stimuli, such as capsaicin (Yang et al., 2014), astringent compounds (e.g., aluminum sulfate, Bajec & Pickering, 2008; Thibodeau et al., 2019), metallic salts (e.g., iron (II) sulfate, cupric sulphate; Bajec & Pickering, 2008; Thibodeau et al., 2019), ethanol (Small-Kelly & Pickering, 2020; Thibodeau & Pickering, 2021), and CO_2 levels in saccharose sweetened solutions (Hort et al., 2016).

The variation in individual responsiveness to thermal changes across different TTS phenotypes has been a subject of interest, particularly whether TTs show greater responsiveness to temperature changes than TnTs. Several studies (Bajec et al., 2008; Hort et al., 2016; Thibodeau et al., 2019) indicate that TTs tend to rate thermal stimuli (both warming and cooling) as more intense than TnTs, supporting the hypothesis that they possess greater orosensory and thermal reactivity. TTs were found to respond to temperature changes not only on the tongue but also on non-lingual sites, indicating that their heightened responsiveness might not be limited to oral perception alone (Thibodeau et al., 2019). However, some discrepancies exist in the literature, not finding consistent differences in thermal sensitivity at extraoral sites (vermillion border of the lower lip, and palm) (Green & George, 2004).

5. TTS and taste physiology

The underlying mechanisms of TTS remain unclear. Heterogeneity in responses to thermal stimulation suggests that thermal taste may be mediated by multiple mechanisms, both at the peripheral and central levels (Botha et al., 2021; Skinner et al., 2018). Temperature stimulation may activate gustatory nerve fibres via TRMP5 to elicit thermal sweetness, demonstrating a defined activation range and providing support for a peripheral mechanism (Skinner et al., 2018). In addition to gustatory afferents, thermal stimulation of the oral cavity activates trigeminal somatosensory neurons, which are crucial for detecting thermal and nociceptive inputs across oral tissues. These neurons express thermosensitive TRP ion channels such as TRPV1, TRPM8, and TRPA1, contributing to the perception of thermal sensations independently of classical taste pathways (Lemon, 2021; Lemon & Lemon, 2017). Whilst gustatory fibres like the chorda tympani respond to both thermal and gustatory inputs, their role in cold sensation is modest compared to the more robust activity of trigeminal neurons, indicating functional specialisation across these pathways (Lemon, 2021).

Table 4 summarises, for each taste and chemesthetic perception, the main mechanistic hypotheses, plausible receptor/effector targets, and key evidence, including indicative temperature ranges where available. The text below expands the logic linking receptor/transduction properties, thermal susceptibility, and the psychophysical patterns observed in TTS.

Among all thermally induced tastes, sweet thermal taste is the most well understood, with a relatively well-defined temperature range and strong support for a peripheral mechanism. Sweet transduction primarily involves TAS1R2/TAS1R3 receptors, and lactisol blockade of this receptor complex abolishes thermally induced sweetness, supporting the idea that warming can directly engage this pathway and activate the downstream, temperature-sensitive channel TRPM5 (Green, 2021; Nachtigal & Green, 2020).

Mild cooling does not initially reduce perceived sweetness but may accelerate sensory adaptation, whereas stronger cold (<12 °C) suppresses the initial intensity, indicating that thermal modulation of sweetness reflects both early transduction and within-trial adaptation dynamics (Green & Nachtigal, 2015; Li & Lemon, 2015). In this context, "sensory adaptation" refers to the within-trial decline in perceived sweetness over seconds during sustained thermal activation of the sweet transduction pathway, not to adaptation to a chemical sweetener. TRPM5, which operates over roughly 15–35 °C, has therefore been proposed as a key effector linking temperature to sweet signalling and supporting a peripheral mechanism for thermal sweetness (Talavera et al., 2005, 2007).

Papillae are the primary structures responsible for detecting and transducing orosensory stimuli, as they contain taste buds and neural innervation (see Piochi et al., 2018, for a review). The greater frequency of thermal sweetness reports on the anterior tongue is consistent with the relatively high density of fungiform papillae and dual gustatory–-trigeminal innervation in this region, although direct links between papilla density, taste-bud number, and thermal sweetness remain to be

Table 4
Thermal taste physiology by taste/chemesthetic modality: candidate mechanisms, receptors, and temperature ranges (TTS and receptor activation).

Taste/ chemesthetic perception	Primary mechanistic hypotheses	Candidate receptors / effectors	Indicative temperature range (°C)	Key evidence / notes
Sweet	Thermal modulation of sweet transduction; strong peripheral component with central integration; dual (warming + cooling) pathways	TAS1R2/TAS1R3 → TRPM5; lactisol block; possible TRPA1/TRPM4; GLUT/SGLT transport systems	TTS range: warming ~23–36; also reported in cooling ~34–21 Receptor activation range: TRPM5 15–35	Lactisol abolishes thermal sweetness; anterior tongue more frequently reports sweetness (fungiform density; dual innervation); fMRI/ physiology show temperature–taste interactions; mild cooling speeds sensory adaptation; strong cold (<12 °C) suppresses initial peak
Salty	Intrinsic temperature sensitivity of ENaC; multi-receptor contribution; temperature amplifies chemesthetic irritation > taste	ENaC; TRPV1/TMC4 (hypothesised)	TTS range: cooling ~24–17 and ~ 7; warming ~27–33 Receptor activation range (°C): ENaC activity reported across ~30 → 15	Cooling more often elicits saltiness in TTS ranges (35 → 5 °C); moderate shifts (12–42 °C) minimally change suprathreshold saltiness but modulate irritation; ENaC temperature gating may underlie inter-individual variability
Sour	Acid-sensing channels with cold-nociceptive contribution; potential warm-linked pathways	PKD2L1/PKD1L3; Kir2.1; TRPV4; ASIC; TRPA1	TTS range: often in cooling with peaks ~16–18 Receptor activation range: ASIC/ TRPA1 active at lower temps (nociceptive context)	Citric acid responses align with nociceptive (ASIC/ TRPA1) activation rather than direct thermal modulation; possible warm-induced sour via OTOP1/TRPV4 range (~24–27 °C)
Bitter	Cooling-dominant reports; trigeminal cold/irritation may be misattributed as bitter	TRPA1 (cold/irritation); GPCR bitter pathways; TRPM5 (insufficient alone)	TTS range: peaks around ~16–18 (cooling) Receptor activation range: TRPM5 15–35; TRPA1 ≤ 17 °	No stable activation window like sweet; TRPM5 alone cannot explain asymmetry vs sweet despite both being GPCR-mediated. Warm-evoked bitter tentatively linked to OTOP1 (~24–27 °C) with possible TRPV4 involvement
Umami	Warm-facilitated GPCR pathway with temperature-sensitive downstream gating	TAS1R1/TAS1R3; TRPM5 (modulatory)	TTS range: chiefly in warming ~20–39 (peak ~28) Receptor activation range: TRPM5 15–35	Thermal activation ranges less defined than sweet; likely more complex / less heat-sensitive mechanisms
Metallic	Multimodal sensation (gustatory + olfactory + trigeminal); mechanism unresolved	TAS2R7 (hypothesised); TRPV1 (hypothesised)	TTS range: reported in both warming and cooling (not specified the range) Receptor activation range: no agreed activation window	High prevalence among TTs; physiological basis remains unclear
Minty (chemesthesis)	Cooling-linked chemesthetic pathway (non-gustatory)	TRPM8; TRPA1 (per thresholds reported)	TTS range: not included Receptor activation range (°C): no agreed activation window TRPA1 ≤ 17 (menthol); TRPM8 ≤ 25 (cinnamaldehyde)	Inclusion as a "valid thermal taste" is protocol-dependent/controversial due to chemesthetic nature
Spicy (chemesthesis)	Heat/pungency-linked chemesthetic pathway (non-gustatory)	TRPV1 (heat, capsaicin)	TTS range: not included Receptor activation range: TRPV1 ≥ 42	As above, inclusion is debated; temperature–chemesthesis interplay can confound gustatory attribution

Note: TTS range (°C) reports temperature intervals at which participants perceived the taste/chemestetic perception during TTS determination. Receptor activation range (°C) reports temperature intervals associated with temperature-dependent modulation of candidate receptors/channels.

clarified (Green & Nachtigal, 2015). Warming-induced sweetness aligns with the known TRPM5 activation range, whilst cooling-induced responses may involve alternative pathways such as TRPA1, TRPM4, or GLUT/SGLT-mediated transport systems. This supports the notion of a dual mechanism underpinning thermal sweet taste perception. Beyond peripheral mechanisms, cortical responses further support the integration between temperature and taste: sucrose at 30 °C increases taste neuron activation, while cooling to 16–18 °C suppresses it (Wilson et al., 2013, 2014). Functional MRI (fMRI) show that TTs exhibit stronger cortical responses than TnTs to cold (6 °C) sweet samples, with activity patterns that correlate with perceptual sensitivity to thermode temperature, suggesting that somatosensory and reward-related circuits contribute to thermal sweet taste (Eldeghaidy et al., 2021; Hort et al., 2016).

Regarding salty perception, ENaC, which is expressed in taste receptor cells and responsible for the perception of saltiness (Bachmanov & Beauchamp, 2007), could be involved in thermally induced saltiness because its activation though temperature ranges from 30 °C to 15 °C (Askwith et al., 2001; Chraïbi & Horisberger, 2003). In fact, when a similar temperature range is used in the cooling cycle for TTS evaluation (35 °C to 5 °C), a thermally induced saltiness occurs more frequently than during warming (Talavera et al., 2005). However, it has not yet been possible to identify a defined activation range for thermally provoked saltiness that confirms this hypothesis (Skinner et al., 2018). Moreover, moderate temperature shifts (12–42 °C) produce little change in suprathreshold saltiness or sourness ratings, but reliably modulate accompanying chemesthetic sensations, consistent with temperature-dependent gating of trigeminal TRP channels; thus, temperature appears to amplify irritation more than gustatory intensity in these ranges (Nachtigal et al., 2019). In parallel, ENaCs may possess intrinsic temperature sensitivity, possibly altering Na^+ current flow and contributing to individual variability in thermally induced saltiness (Lemon, 2021). Salty taste responses have also been detected at different temperature peaks—during cooling (24–17 °C and at 7 °C) and warming (27–33 °C)—suggesting a multi-receptor involvement, possibly including TRPV1 and TMC4, and overlapping with metallic perception pathways (Botha, 2024).

Sour taste mechanisms remain less clear, with suggested roles for potassium channels (PKD2L1, PKD1L3, Kir2.1) and TRPV4 as potential receptors for acidic perception (Challis & Ma, 2016; Matsumoto et al., 2019; Ye et al., 2016). Temperature-sensitive responses to citric acid are more consistent with the activation of nociceptive pathways such as ASIC or TRPA1, rather than with direct thermal modulation of sour taste (Nachtigal et al., 2019). Thermally induced bitter and sour sensations are predominantly reported during cooling, with peaks around 16–18 °C. TRPA1—a cold-sensitive ion channel associated with chemosensory irritation—may mediate these perceptions or generate sensations that are perceptually misattributed to bitterness or sourness. OTOP1 may also be implicated in warm-induced bitter or sour sensations, particularly in the 24–27 °C range aligned with TRPV4 activation (Botha, 2024).

Despite the potential involvement of TRPM5 in bitter and umami

transduction, thermally elicited bitterness lacks a consistent activation range and is mostly experienced during cooling. Even if the highly temperature-sensitive and heat-activated nonselective cation channel TRMP5 may play a key role in the transduction also of bitter and umami taste, thermally elicited bitterness lacks a clear temperature range and is predominantly reported during cooling cycles (Skinner et al., 2018). This discrepancy, alongside the structural rigidity of GPCRs like TAS1R1/TAS1R3 for umami, suggests that thermal modulation of these qualities involves more complex or less heat-sensitive mechanisms (Green, 2021).

Asymmetrical thermal responsiveness between sweet and bitter stimuli—both transduced via GPCRs—indicates that TRPM5 alone cannot fully explain thermal taste phenomena. Instead, multiple receptors and effectors may contribute to this modulation (Lemon, 2021).

Umami also lacks defined thermal activation ranges, complicating discussions of its mechanisms.

For metallic perception, debates persist regarding whether it constitutes a taste or a multimodal sensation involving gustatory, olfactory, and trigeminal pathways (Epke et al., 2009; Lawless et al., 2005). Metallic sensations induced by temperature changes may involve channels other than TRMP5, such as TAS2R7 and TRPV1 (Emir, 2017; Riera et al., 2007, 2009; Wang et al., 2019).

These sensations were more often reported during cooling and warming, aligning with activation patterns of TRPM5, TRPA1, and TRPV1 (Botha, 2024).

Instead, the receptors responsible for spicy and minty sensations, activated by both temperature and chemical stimuli, could be TRPV1 ($\geq$42 °C and capsaicin), TRPA1 ($\leq$17 °C and menthol), and TRPM8 ($\leq$25 °C and cinnamaldehyde; (Dhaka et al., 2006; Julius, 2013), whose activation ranges would fall within the temperatures of cooling and warming cycles (Thibodeau et al., 2020).

In addition to TRPM5, other thermosensitive channels such as TRPM8 and TRPM2 contribute to oral thermal perception and may modulate taste indirectly. TRPM8, expressed in small and medium-diameter neurons, mediates cold perception and analgesia, whilst TRPM2 and TRPV4 are responsive to innocuous warmth and may influence oral temperature preferences and multisensory integration (Kashio & Tominaga, 2022).

Chemosensory perception may vary among individuals depending on several factors, such as gender, age, ethnicity, or previous exposure. Much of this variation can be explained by genetic differences in chemosensory receptor genes that determine their level of function (Feeney et al., 2021). Therefore, further investigation of genetic differences and variability in chemosensory genes could help to understand a possible correlation between the TTS and differences in perception, and thus in liking and intake of food and beverages.

By examining common genetic variation in relation to TTS, no association between TTS and any of the SNPs tested was found, nor with TRPM5 copy-number variation, leaving the genetic basis of TTS unresolved (Bering, 2012). Because participants were analysed as a single TT group—rather than stratified by reported taste identity or temperature regime—these null findings do not rule out subtype-specific genetic effects. Similarly, polymorphisms in TRPV1 (rs8065080) and TRPA1 (rs11988795) could contribute to inter-individual differences in trigeminal and thermal perception. In particular, genomic variability in the TRPV1 gene (rs8065080) (Aroke et al., 2020) has been associated with alterations in various pain conditions and with alterations in salty taste sensitivity and salt preference whilst TRPA1 (rs11988795) (Schütz et al., 2014) has been associated with enhanced sensitivity to cold-induced pain, suggesting a broader role in modulating sensory experiences.

6. Relationship between TTS, socio-demographic characteristics, personality traits and phenotypes

6.1. Effect of socio-demographic characteristics

Only a few studies have examined the association between TTS and gender, age, and ethnicity and determined the relative effects of these factors on perceived taste intensity. Table 5 offers an overview of the participants in the various studies and how their responses to thermal stimulus were classified as TTs, TnTs, NC.

No gender differences have been found between TTs and TnTs (Bajec & Pickering, 2008; Botha et al., 2021; Pickering & Kvas, 2016; Pickering, Moyes, et al., 2010; Thibodeau et al., 2019; Yang et al., 2014, 2020). In fact, several studies limited recruitment to females in order to remove sex as one of the known sources of variation in human olfaction and orosensation (Mitchell et al., 2019; Thibodeau & Pickering, 2021). Taken together, there is no clear evidence for sex-related differences in TTS prevalence, nor for sex × TTS interactions in orosensory responsiveness.

In terms of age, no association with TTS was found (Bajec & Pickering, 2008; Pickering & Kvas, 2016), whilst one investigation reported TTs were, on average, 2.2 years younger than TnTs (Thibodeau et al., 2019). The latter cohort was predominantly composed of young adults, which may limit sensitivity to age effects in older decades and constrains generalisability (Thibodeau et al., 2019). By contrast, a later analysis indicated that TT participants tended to be slightly older than TnTs; however, age did not emerge as a reliable predictor of TTS (Botha, 2024). Taken together, age effects may be sample-composition dependent and should be tested with age-stratified analyses in broader cohorts.

Regarding ethnicity, no difference in the proportion of TTs and TnTs was found between Caucasian and non-Caucasians (Thibodeau et al., 2019). Contrarily, in the study by Bajec and Pickering (2008), in which participants evaluated the intensity of low and high levels of astringent, salt, sweet, sour, bitter and metallic stimuli in aqueous samples, it was found that TTS*ethnicity interactions for the solutions with low astringency and low metallic level were significant. Instead, Yang et al. (2020), analysing a sample of 223 participants, suggested that ethnicity also contributes to this variation. In fact, when comparing Caucasian with Asian populations, 51 % of Asians were classified as TTs, reporting a taste sensation during warming or cooling trials (with only 30 % TnTs among Asians), whilst a much lower percentage of TTs (33 %) and a much higher percentage of TnTs (57 %) were observed among Caucasians (Yang et al., 2020). Ethnicity-related findings should be interpreted in context: the categories used are broad and mask substantial within-group heterogeneity. Country context (e.g., New Zealand, the UK, and Canada) may also shape reporting via differences in linguistic conventions, sensory training practices, and food culture. Between-group contrasts may reflect not only methodological differences but also non-methodological factors such as bilingualism and language of testing, the semantics of taste descriptors and scale anchors, dietary acculturation, culinary practices, and habitual exposure to temperature-modulated foods and beverages.

Semantics, usage of taste descriptors and scale anchors can differ between first language (L1) and second language (L2), and bilingual participants may show language-dependent neural response patterns (Sulpizio et al., 2019); these factors could shape reported intensity/quality independently of chemosensory biology.

6.2. Effect of personality traits

In addition to gender, age, and ethnicity, psychosocial characteristics have also been examined. Evidence linking TTS to personality is emerging and mixed. Relative to TnTs, TTs reported lower food neophobia, higher food involvement, and a more active imagination (Yang, 2015). When evaluating personality using the five-factor model, higher

Table 5
Overview of subjects' classification.

Reference	Subjects n.	Gender	Age	Smoke status	TTs	TnTs	NCs
Cruz & green, 2000	24	16 F; 8 M		Not specified	21 reported at least one taste quality 19 14 F; 5 M reported two or more tastes at one or more sites along the anterior edge of the tongue.	Not applicable	
Green & George, 2004	95	63 F; 32 M	Range: 18–45	Non smokers	14	14	
Green et al., 2005	exp 1: 29 exp. 2: 46 exp. 3: 41	23 F; 6 M 29 F; 17M 27 F; 14 M	Range: 18–45	Non smokers	25 tongue tip and 20 circumvallate papillae region	21 tongue tip and 14 circumvallate papillae region	
Bajec & Pickering, 2008*	126	84 F; 42 M	Range: 18–68		24 16 F; 8 M	49 35 F; 14 M	
Bajec & Pickering, 2010*	132	84 F; 43 M	Range: 18–68		26 16 F; 10 M	50 36 F; 14 M	
Pickering, Moyes, et al., 2010*	56	eligible for TTS 23 F; 17 M		Non smokers	20	20	
Pickering, Bartolini, et al., 2010*	53	27 F; 26 M	Range: 19–49	Non smokers	20 9 F; 11 M	20 10 F; 10 M	
Bajec et al., 2012*	44			Non smokers	24 17 F; 7 M	20 12 F; 8 M	
Bering et al., 2014*	53	36 F; 17 M	Mean age ± SD: 26.5 ± 9.7	Non smokers	28	25	
Yang et al., 2014	204	132 F; 72 M	Mean age: 42 Range: 16–75		56	61	87
Hort et al., 2016	52	32 F; 20 M	Mean age ± SD: 35 ± 7		12 8 F; 4 M	40	
Pickering & Klodnicki, 2016*	44	89 F	Range: 17–40	Non smokers	23	21	
Pickering & Kvas, 2016*	87	33 F; 54 M	≥19	Non smokers	27	28	32
Pickering et al., 2016a 2016*	44		Range:18–44		25 15 F; 10 M	19 8 F; 11 M	
Eldeghaidy et al., 2018	60	43 F; 17 M	Range:18–60		29	26	5
Yang et al., 2018	60		Range:20–62		30	30	
Skinner et al., 2018	85		Range:19–40	Non smokers	28 % - 36 23 F; 13 M	51 %	21 %
Mitchell et al., 2019*	117	117 F	Range:18–35		22	20	53
Thibodeau et al., 2019	708	484 F; 223 M; 1 not declared	Range:18–75		218	183	307
Small-Kelly & Pickering, 2020*	60	109 F; 51 M; 4 not declared	Mean age ± SD: 23.2 ± 5.9		31 21 F; 9 M; 1 not declared	29 17 F; 13 M	
Yang et al., 2020	223	160 F; 63 M	Range:18–65	Non smokers	86 F 62; M 24	109 F 76; M 33	28 F 22; M 6
Thibodeau et al., 2020	781	556 F; 223 M	Mean age ± SD: 25.1 ± 9.4		254	207	323
Eldeghaidy et al., 2021	24	14 F; 10 M	Mean age ± SD: 25 ± 7		12	12	
Thibodeau & Pickering, 2021	142 After session 1 = 135	142 F	Range:18–40	Non smokers	Session 2 = 29 Session 3 A = 21 Session 3B = 22 Session 3C = 22 Session 3D = 21 Final = 18	Session 2 = 19 Session 3 A = 13 Session 3B = 14 Session 3C = 15 Session 3D = 14 Final 13	Session 2 = 54
Botha et al., 2021	140 of which 132 phenotyped	76.5 F 22.7 % M 0.8 % non-specified	Mean age 34.2		Traditional protocol A = 30 Traditional protocol B = 20 Cobined protocol C = 38	Traditional protocol A = 59 Traditional protocol B = 86 Combined protocol C = 84	Taditional protocol A = 30 Traditional protocol B = 26 Combined protocol C = 10
Pickering & Pickering, 2022	471	74 % F 26 % M	Range:17–75 Mean age ± SD: 23.0 ± 7.7		121	76	176

Note: exp.: experiment; TTs: Thermal tasters; TnTs: Thermal non taster; NC: Not classified subjects.
The blanks are due to some information not found in the articles.
* Data from the studies marked with an asterisk were included in the Thibodeau et al., 2019 and 2020 analyses in order to look at trends in a large dataset.

Openness to Experience was observed among TTs, with no difference in Extraversion (Yang, 2015). By contrast, higher scores on both personality dimensions of Extraversion and Openness to Experience were reported for TTs. Moreover, cluster analysis revealed that differences among TT subtypes extended beyond sensory perception to include personality traits such as agreeableness and conscientiousness (Both, 2024). Additionally, indirect support comes from work using the Foodie Index to capture enthusiasm and engagement with food. Indeed, individuals with higher Foodie Index scores ("foodies") tended to be more extraverted and more open to experience, and were more likely to be TTs (Pickering & Pickering, 2022). These findings suggest that TTS, especially when subtyped, reflects broader individual differences and contributes to food preferences through a complex interplay of sensory sensitivity, personality, and dietary habits.

6.3. Effect of PROP taster status and fungiform papillae density

Individual difference in the perception of 6-n-propylthiouracil (PROP) bitterness is the most studied source of individual variation in taste perception. The gene contributing to PROP perception, identified as TAS2R38, is characterised by two molecular forms (PAV and AVI) (Tepper et al., 2014, 2017). The relationship between TTS and PROP taster status (PTS) arises from perceptual and behavioural parallels in reactivity to PROP and TTS, suggesting a potentially shared genetic basis (Bajec & Pickering, 2008; Eldeghaidy et al., 2018; Pickering, Moyes, et al., 2010; Yang et al., 2014). In early studies, it was found that PROP supertaster status may be associated with a higher density of fungiform papillae (Bartoshuk et al., 1994), and presumably having more tympanic cords and trigeminal nerve fibres, thus partially explaining increased taste and trigeminal sensitivity compared to the other two groups (Bajec & Pickering, 2008). However, the relationship between PTS and fungiform papillae density is still controversial (Dinnella et al., 2018; Piochi et al., 2021b), as more recently highlighted. No significant relationship was found with TTS and fungiform papillae count in the only study exploring this topic (Eldeghaidy et al., 2018).

Studies investigating the relationship between PTS and TTS suggest that the phenotypes are independent, not sharing the same mechanism and no evidence of their interaction found at the phenotypic level (Bajec & Pickering, 2008, 2010; Eldeghaidy et al., 2018; Pickering, Moyes, et al., 2010; Thibodeau et al., 2019; Yang et al., 2018). The possible association between PTS and TTS from a genetic perspective was examined to determine whether the perceptual and behavioural similarities of the markers had a common genetic origin (Bering et al., 2014). The association between TTS and genotype of individual TAS2R38 Single Nucleotide Polymorphisms (rs713598, rs1726866, and rs10246939) known to be associated with PROP reactivity and their combinations were analysed (Bering et al., 2014). TTS was not associated with these Single Nucleotide Polymorphisms of TAS2R38, reinforcing the indication of no association between PROP reactivity and TTS.

In more recent work, no direct relationship was observed between TTS or thermal taste response clusters and PROP taster classification. However, TT participants tended to report higher PROP bitterness intensity, whilst participants with lower PROP ratings were less likely to be TTs (Botha, 2024). These findings suggest that general sensitivity to bitterness, rather than PROP taster status per se, may be more closely associated with thermal taste responsiveness.

Only two studies have investigated TTS and fungiform papillae density, with no relationship identified (Bajec & Pickering, 2008; Eldeghaidy et al., 2018). A purely peripheral explanation based on higher innervation density therefore seems unlikely to account for TT advantages (Green & George, 2004). However, although scientific evidence has shown the independence of the two phenomena, (Yang et al. (2014) found that individuals who were hypersensitive to PROP were not affected by being a TT, but for PROP medium tasters, characterised by a moderate number of papillae, being a TT may impact perceived taste intensity more than TnTs. Overall, for the evidence available so far, PROP taste status and TTS seem to be independent phenotypes, and fungiform papillae density also appears independent of TTS, although larger studies are warranted to confirm these conclusions.

7. Influence of TTS on food and beverage perception and preference

7.1. Influence of TTS on beverage perception, preference and emotions

Most studies have examined how TTS influences perceived taste and flavour intensity in beverages; comparatively fewer have addressed liking, preference, or emotions. Evidence included beer (Mitchell et al., 2019; Pickering, Bartolini, & Bajec, 2010; Small-Kelly & Pickering, 2020); wine (Pickering & Kvas, 2016; Pickering, Moyes, et al., 2010); cider (Small-Kelly & Pickering, 2020), binary solutions of ethanol and a tastant (Thibodeau et al., 2021), and strawberry drink served at different temperatures (Yang, 2015). The prevailing hypothesis suggests that **TTs** perceive orosensory stimuli more intensely than **TnTs**, particularly in liquid matrices where the involvement of multiple receptors may amplify the effect of thermal taste (Pickering et al., 2016; Thibodeau et al., 2019).

Several studies have shown that TTs tend to perceive higher intensities of key sensory attributes in alcoholic beverages compared to TnTs. Specifically, it has been consistently found that TTs rated the bitterness, sourness, sweetness, astringency, carbonation, and overall flavour intensity higher than TnTs across a range of beer, cider, and wine samples (Pickering, Bartolini, et al., 2010; Small-Kelly & Pickering, 2020; Mitchell et al., 2019; Pickering, Moyes, et al., 2010). Using temporal check-all-that-apply (TCATA), it was also found that TTs reported astringency, bitterness, and carbonation more frequently, particularly at colder serving temperatures (6 °C) (Mitchell et al., 2019). These results are consistent with findings that TTs experienced greater maximum intensity and longer duration of astringency from aluminum sulfate solutions served at 35 °C compared to 5 °C (Bajec et al., 2012). Collectively, these studies support the notion that TTS is an important factor influencing the multisensory perception of complex beverages.

The composition of a beverage, including ethanol concentration, may influence how TTs and TnTs perceive orosensory attributes. TTS might influence the perception of ethanol-related sensory attributes (non-dominant: sweetness and astringency; dominant: bitterness and burning/tingling) (Thibodeau & Pickering, 2021). Differences in alcoholic beverage liking based on TTS were only found when ethanol was at higher concentrations (e.g., dry red wine, spirits) but not lower concentrations (cider, white wine, beer; Bajec, 2011, Pickering, Moyes, et al., 2010, Small-Kelly, 2018). Despite no differences in preference for beer, TTs rated the importance of taste significantly higher when purchasing beer than TnT (Small-Kelly, 2018). Thus, liking and preference are more complex phenomena that cannot be explained by TTS alone.

In addition to the hedonic responses, emotions could influence consumer preferences (Kytö et al., 2018). It has been shown that the combination of pleasantness and emotions can predict consumer choices more than pleasantness itself, as emotions can influence food choices and consumption and vice versa (Dalenberg et al., 2014; Köster & Mojet, 2015). By examining the relative effects of some phenotypic combinations on emotional response to beer, it was found that TTS and PTS were associated with a different nature of emotions (Yang et al., 2018). Specifically, it would appear that TTS is associated with negative emotions,

whilst PTS is related to positive emotions, although it is unclear why it would elicit these discriminating emotions. In addition, the results of this work revealed a more pronounced effect of PTS in TnTs.

7.2. Influence of TTS on solid food perception and preference

The relationship between TTS and preference for solid foods remains less explored compared to beverages. This is probably due to the fact that liquids, more than solid foods, might involve more receptors in the mouth promoting a clearer taste "advantage" among TTs, so liquids have a better chance to activate thermal perception (Pickering et al., 2016; Thibodeau et al., 2019). Moreover, several matrix-level properties plausibly make beverage effects easier to detect: liquids more uniformly coat oral surfaces, typically produce larger changes in tongue temperature due to higher water content and heat capacity, and involve longer continuous contact than many solids; by contrast, mastication, salivary dilution, and lower moisture in solids can limit the magnitude and duration of lingual temperature change, reducing opportunities for thermally elicited sensations to emerge.

Across solid-food categories (e.g., raw vegetables, dairy, sweets, textured foods, salty snacks), intensity differences between TTs and TnTs are not consistently observed. In one dataset, taste-attribute intensity did not differ between TTs and TnTs, yet TnTs showed greater liking for foods classed as "aversive" (dominant bitter, sour, and/or astringent). Thus, the observed liking gap cannot be attributed to measured intensity differences in that dataset and likely reflects other drivers—e.g., texture and oral processing preferences, product composition, lower lingual temperature change in solids, or learned/affective tolerance to aversive qualities (Pickering et al., 2016; Pickering & Klodnicki, 2016). This distinction underscores that perceived intensity and hedonic response are related but separable constructs; differences in liking may emerge even when intensity ratings converge.

Food-related behaviours provide additional nuance. TTs report practices consistent with higher responsiveness to chemical stimuli and condiments (e.g., more frequent addition of salt or heat, greater enjoyment of burn), with some differences mapping onto TT subgroups; for example, individuals associated with metallic and salty thermal tastes were less likely to add salt (Botha, 2024). However, no systematic differences have emerged for several variables, including food neophobia, sweet-liking status, fatty acid reactivity, or general liking for spicy foods, suggesting that not all dietary behaviours are tied to thermal taste responsiveness (Botha, 2024; Yang et al., 2020).

Another important factor in food preference appears to be texture. TnTs were found to have a higher preference for creamy and grainy food textures compared to TTs (Pickering & Klodnicki, 2016). Specifically, TnTs rated dairy products included in the "cream orosensory group" more favorably than TTs, and also exhibited a more positive response to grainy foods. However, the latter finding should be interpreted with caution, as the grainy food group in this study included only a single item (Pickering et al., 2016). The results align with a self-reported food-liking survey which found that TnTs showed lower liking for dairy products and greater preference for cooked fruits and vegetables compared to TTs (Bajec & Pickering, 2010). Consistent with these findings, texture preferences were also explored using the oral processing behaviour questionnaire developed by Jeltem et al. (2015) and Jeltema et al. (2016). Participants classified as "crunchers"—those who prefer crisp or crunchy textures—were more frequently TTs, suggesting a possible link between oral texture preferences and thermal taste sensitivity. Oral processing subgroups did not predict membership in a specific TT cluster, indicating that this behavioural trait may be more closely related to general TT status rather than to the specific taste-temperature profiles defining each cluster (Botha, 2024). The influence of TTS on food perception may have broader implications for dietary behaviours and health. Differences in taste sensitivity and texture preference may affect food choices, potentially influencing dietary patterns and even health risks related to fat, sugar, and salt consumption (Pickering et al., 2016). However, no direct association has been found between TTS and body mass index (BMI) or waist size (Bajec & Pickering, 2010).

8. Limitations and gap

Thermal tasting is an emerging sensory phenotype that may influence consumer behaviour yet remains understudied. The present review of the scientific literature reveals several unresolved issues and areas requiring further investigation. Table 6 offers an overview of all limitations and gaps identified in the scientific literature during the analysis of this topic.

One of the main limitations identified is the heterogeneity of classification methods and the clear need for a standardised methodology across researchers to enable more effective, collaborative work and cross-cultural comparison. Starting from the protocol itself, methodological heterogeneity is evident: different thermode shapes and surface areas (and, consequently, different modes of stimulating the lingual surface); non-aligned temperature ramps and plateaus; and differing heating/cooling sequences. Added to this is, the lack of uniformity in classification rules, which vary in minimum threshold (e.g., "above weak"), replication requirements (same site/quality), the requirement for responses in both temperature regimes, or the use of adjudication replicates. Scale format, the label set, and training are not always standardised. Moreover, response flow (e.g., immediate end-of-trial rating versus an initial yes/no gate; TCATA versus intensity ratings) can change what is actually reported as a thermally elicited taste. These factors determine what counts as a valid thermally induced taste and, therefore, TT/TnT/NC assignment, and the large NC proportions complicate cross-study comparisons and mechanistic inference.

A related limitation is that NC groups are often treated as a borderline category and simply excluded from analyses, rather than being systematically characterised (e.g., based on the type of sensation reported, intensity, or consistency of response). This practice makes it difficult to determine whether NCs mainly reflect a true absence of thermal taste, borderline responders, or artefacts driven by the protocol and response format. This limits the development of refined, subgroups-sensitive classification patterns.

From a linguistic and country-context perspective, almost all studies have been conducted in English-speaking contexts; the semantic transparency of instructions and anchors may vary across languages and cultures, with potential impacts on classification. In addition, small and non-representative samples (a prevalence of young adults, and in some cases female-only cohorts) limit generalisability across age and sex.

At the physiological level, the absence of well-defined mechanisms complicates delineation of the thermal taste phenotype and contributes to inconsistencies in TT classification. Hypotheses are more focused for sweetness, but remain unresolved for saltiness, sourness, and bitterness, and especially for metallic sensations; the inclusion of "spicy" and "minty" as valid tastes remains controversial due to potential chemesthetic confounding. Beyond receptor-level candidates, individual differences in general thermal sensitivity—both intra-oral and extra-oral—have only been sparsely examined, even though existing data suggest that TTs and TnTs can also differ in perceived intensity of temperature changes outside the mouth. This limits current understanding of how TTS relates to broader thermosensory phenotypes. Genetic evidence is preliminary: one study on common variants found no associations when TTs were analysed as a single group, leaving open the possibility of subtype-specific effects by thermal taste profile (Bering, 2012). Foods and beverages are complex matrices with different physical and chemical properties (e.g., water content, viscosity, fat content) that can influence flavour release, thus modulating the availability of a ligand that interacts with a target receptor (Feeney et al., 2021). Moreover, beverages—even at room temperature—tend to induce larger changes in lingual temperature due to higher heat capacity and more extensive oral coating, which facilitates observation of

Table 6
Mapping gaps in the literature on TTS, outlooks, and possible methodological approaches.

Topic	Key Gap / Limitation	Future Research	Recommended Approach
Protocol	No standard protocol (thermode geometry, stimulation sites, ramps/holds, sequence); non-uniform scales/ labels/training → non-comparable TT/TnT/NC estimates	Validate a shared, standard protocol that also standardises response collection	• Large, cross-cultural, multi-lab study with shared data resources • Use combined warming–cooling sequence when appropriate • Shared gLMS/ gVAS training manual; harmonised label sets (including an explicit stance on "metallic," "spicy," "minty")
Classification	Heterogeneous criteria (cut-offs, replication rules, temperature regime) → high NC and potential misclassification	Define unified criteria and an explicit NC classification; evaluate taste-specific subgroups	• Embed clear, defined classification rules (thresholds, replicability, regime) in the protocol • Implement RapCoTT with TCATA • Stratify participants based on taste-specific evaluation (e.g. sweet/bitter/ umami; warming vs cooling)
Language & country	Studies mostly in Anglophone contexts; possible semantic drift in instructions/ anchors	Multilingual validation and cross-country replication	• Pre-specify sampling frames • Collect detailed language histories (L1/L2, proficiency, age of acquisition) • Provide L1 materials with translation/back-translation and cognitive interviewing • Standardise descriptors/ anchors and classification criteria across sites, with multilingual replication
Sampling	Small, young, sometimes female-only cohorts; limited diversity	Expand participant datasets; cross-cultural studies	• Recruit larger, age- and sex-balanced, ethnically diverse cohorts • Document cultural, linguistic, and dietary exposure profiles
Physiology	Absence of well-defined mechanisms for most tastes and chemesthesis; metallic unresolved; spicy/minty contested	Studies on mechanisms and receptors; studies on individual sensitivity (e.g. temperature); potential validation/ inclusion of chemesthetic perceptions	• Design studies that dissociate gustation from chemesthesis by using trigeminal controls (e.g., menthol, capsaicin, CO_2) with separate irritation ratings, analysed with time-resolved profiles (TCATA) • Test with real foods that naturally evoke warmth/cooling/ pain (e.g., spicy products) to relate TTS to everyday exposure Test with real foods that evoke heat/ cooling/pain (e.g., spicy)
Genetics	Limited work; TT often treated as a single group	Genotype–phenotype studies stratified by thermal subgroups; investigate variability in chemosensory genes	• Subgroup-aware analyses (e.g., sweet/bitter/ metallic; warming vs cooling) • *Re-*examine TRPM5 and TRPV1/ TRPA1 variants, alongside other chemosensory genes • Use larger, diverse cohorts with transparent variant selection and reporting
Real food matrices	Emphasis on aqueous solutions; few real-food studies	Real-food studies; identify factors discriminating TTs vs TnTs (e.g., texture, bitterness, thermal sensitivity)	• Ecological tests on real foods and beverages, systematically modulating structure (e.g. texture, taste profile) and serving temperature • Control mastication and saliva incorporation; support these studies with IRT and, where relevant, virtual-taste paradigms

TT–TnT differences; many solid foods, with lower water content and greater saliva incorporation, produce more modest changes in lingual temperature and, therefore, less pronounced effects.

Finally, the stimulus domain is imbalanced: there is a strong emphasis on aqueous solutions and relatively little research on real foods. While such solutions are useful for isolating specific sensory responses and linking them to genetic variants, they may not reflect real-world sensory experience.

9. Future perspectives and research

The presence of several limitations and gaps in the literature offers clear opportunities to expand research and address aspects that remain uncertain or unexplored. Table 6 summarises potential future studies and recommended methodological approaches to close the identified knowledge gaps.

A standardised protocol is highly desirable, covering scale training and use, thermode geometry, stimulation site(s), temperature ramps and holds, and a combined warm–cool sequence when appropriate, together with clear and defined classification rules, and a preference for real-time

response collection (e.g., TCATA) to reduce memory bias and scale artefacts. The introduction of RapCoTT represents a significant methodological advance that addresses many limitations of earlier approaches; wider adoption could improve between-study comparability and provide a more detailed understanding of individual differences in thermal taste perception (Botha et al., 2021). Future studies should build on this by using larger, age- and sex-balanced cohorts and by segmenting TTs according to the sensations elicited during lingual thermal stimulation, such as adopting a taste-specific stratification of TTs, TnTs, and NCs (Chirilli et al., 2026). Validation of a standardised protocol could be pursued through a large, cross-cultural, multi-lab study with shared data resources.

Future studies should also pre-specify sampling frames, record detailed language histories (first/s language, proficiency, age of acquisition), administer instructions and descriptors in participants' first language with translation/back-translation and cognitive interviewing, and standardise descriptors/anchors and classification criteria across sites with multilingual replication. This will help disentangle cultural–linguistic influences from physiological variation and rigorously test whether TTS contributes to observed cross-ethnic differences in food choice.

On the physiology front, taste-specific tests that distinguish gustatory and chemesthetic pathways are needed, with particular attention to metallic perception. Genotype–phenotype studies should stratify by thermal subtype (e.g., sweet-, bitter-, metallic-dominant; warming- vs cooling-dominant) rather than aggregating all TTs into a single group, and should re-examine TRPM5 alongside TRPV1/TRPA1 variants (Bering, 2012).

Future research on genetic variations should consider specific SNPs linked to known chemosensory and temperature-sensitive pathways. For instance, variations in TRPM5 (single nucleotide polymorphisms, namely rs886277, rs2301696) may influence the intensity of thermally elicited tastes, given TRPM5 role in temperature-dependent taste transduction (Ketterer et al., 2011). Exploring these SNPs could clarify the genetic mechanisms underlying individual variation in thermal taste and potential interactions between predisposition and sensory experience.

Preferences for spicy and hot foods may relate to individual differences in nociceptive heat thresholds. People with higher heat pain thresholds are more likely to enjoy spicy foods and hot drinks, possibly due to TRPV1-mediated responses to heat and capsaicin (Defrin et al., 2021). Overall, individual differences in oral thermosensation are unlikely to be explained by a single factor (e.g., receptor density or a single TRP channel), but rather by combined effects of trigeminal innervation, spatial distribution of nerve endings, and central mechanisms (Manrique & Zald, 2006). Recent studies have begun to explore potential peripheral and central mechanisms involved in TTS, and their possible interactions (Thibodeau et al., 2020). Electrophysiological studies in rats have shown that temperature itself can modulate taste responsiveness at the level of peripheral neurons, suggesting a direct thermosensory influence on taste encoding in early stages of signal processing (Breza et al., 2006). These findings support the continuation of research on the neurophysiological basis of thermal taste, including the possible presence of structural differences between TTs and TnTs. Moreover, a moderate association has been reported between PROP taster status and suprathreshold cold sensitivity on the tongue, suggesting a limited - but possible - overlap between thermal and gustatory sensitivity mechanisms.

Consumers' behavioural choices and preferences warrant further study. Using real food matrices could clarify the role of TTS in shaping preferences by targeting parameters that the literature already flags as potentially discriminating between TTs and TnTs. In particular, it would allow assessment of whether texture constitutes a discriminating factor in hedonic responses between TTs and TnTs (Bajec & Pickering, 2010) and for evaluation of potential differences in perception of bitter-eliciting foods across thermal phenotypes, given the higher bitterness ratings typically reported by TTs (Pickering et al., 2016; Small-Kelly & Pickering, 2020). More work is also needed to assess whether TTS-linked perceptual differences contribute to dietary patterns and long-term health outcomes. Product temperature preferences may help interpret differences in responsiveness and sensitivity among TTs. With real food matrices, it is advantageous to manipulate serving temperature and water content to modulate lingual temperature change, to control mastication and saliva incorporation, and to test whether larger lingual temperature variations predict larger TT–TnT differences (Bajec et al., 2012; Mitchell et al., 2019).

In addition to studies directly motivated by the identified limitations, further exploratory directions can be envisaged that, while not strictly gap-driven, may help to clarify TTS mechanisms and potential applications.

In fact, some technological advances now could allow more precise probing of thermal–taste interactions. Infrared thermography (IRT), a non-invasive, contact-free technique for tracking tongue-surface temperature during real food and beverage consumption (Lv et al., 2019) can quantify lingual thermal change in relation to perceived intensity. Future studies could use IRT to systematically compare lingual temperature dynamics between TTs and TnTs across liquid and solid foods, and test whether larger temperature shifts predict stronger thermally elicited sensations. Recording baseline temperature, immediate thermal shift, and recovery remains informative, but should be integrated with perceptual data through mixed-effects or mediation models tailored to TTS. In real-food tasks, IRT can track tongue-temperature dynamics during consumption and relate them to perceived flavour, as shown by positive associations between tongue temperature and sweetness/vanilla intensity (McNeill et al., 2025).

Beyond the lab, digital taste technologies such as the Thermal Taste Machine (Karunanayaka et al., 2018), Virtual Taste (Ranasinghe, 2024), and *E*-Taste (Ullah et al., 2022) aim to evoke specific taste sensations through targeted heating and cooling. While the concept is intriguing, current evidence is weak and methods lack rigor. Small sample sizes and limited controls raise concerns about reproducibility. If reducing sugar or salt without compromising flavour proves feasible, commercial interest will likely be strong. However, progress depends on using robust and controlled protocols to measure the strengths and limitations of the technology, which can best be achieved through partnerships between technology developers, psychologists, and sensory scientists. With such collaboration, these early prototypes could evolve into reliable tools for research and application.Thermal stimuli also interact with oral–motor functions. Findings that swallowing comfort and initiation timing vary with temperature or taste quality (Gatto et al., 2021; Miyaoka et al., 2006) highlight broader sensorimotor impacts of oral stimulation. Since warm/cool elicitation cycles may induce discomfort in some participants, potential pain-related confounds should be considered analytically. Moreover, since most tested foods have been served at or near room temperature, they may not fully capture the interactions that occur with truly cold or hot products. Liquids typically induce greater tongue temperature changes than low-moisture solids, which can amplify TT-TnT differences, especially in beverages. Saliva also matters: being at body temperature, greater incorporation into a solid bolus can blunt tongue cooling or warming, further reducing temperature-driven effects (Thibodeau et al., 2019). Thermal and chemosensory cues could jointly shape oral sensorimotor responses; ease of swallowing does not necessarily mediate TTS per se, but it is plausible that thermal profiles of real foods and drinks can influence the expression of thermal tastes.

Future work could investigate whether TTS may influence other temperature-sensing mechanisms and associated genes unrelated to taste perception, as also demonstrated by Thibodeau et al. (2019), in which TT and TnT differ in the intensity of temperature perception both inside and outside the oral cavity. Thus, it can be hypothesised that TTs may experience thermally induced flavours during the consumption of cold or frozen products. In the same way, TTs may experience thermally induced tastes when consuming hot products. Thus, it would be worth investigating if experiencing the thermally-elicited tastes during normal

eating and drinking is the cause of the increased responsiveness of TT compared to TnT. Alternatively, TT might just react more strongly that TnT to taste sensations using a central gain mechanism. It might therefore be interesting to understand how the phenotype might be related to liking and consumption.

10. Conclusion

The purpose of this review was to critically examine the current scientific knowledge on TTS, highlighting both the main findings and the substantial gaps that remain. By systematically mapping the literature, this work goes beyond a descriptive synthesis, offering an analysis of the methodological, physiological, and applicative limitations that still hinder the full understanding of this sensory phenotype. One of the most pressing challenges concerns the unclear physiological mechanisms underlying thermal taste perception. Addressing this fundamental issue could pave the way toward resolving many of the inconsistencies and limitations identified in TTS classification, thereby improving the reliability and comparability of future studies. This review also emphasises the importance of adopting standardised and inclusive classification methodologies, capable of capturing the heterogeneity of oral sensory responses, and of integrating recent advances in neurophysiology, genetics, and digital sensory technologies. By shedding light on the complex interplay between thermal taste sensitivity, food behaviour, and individual traits, this work contributes to redefining the role of TTS not only as a psychophysical curiosity, but as a potentially relevant factor in shaping food preferences, dietary patterns, and possibly diet-related health outcomes. Ultimately, this review provides a structured foundation and a set of critical insights to support and guide future interdisciplinary research, aiming to clarify the mechanisms and implications of TTS and to fully recognise its value within the broader field of sensory and nutritional sciences.

CRediT authorship contribution statement

Chiara Chirilli: Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Maria Piochi:** Writing – review & editing, Conceptualization. **Qian Yang:** Writing – review & editing, Conceptualization. **Margaret Thibodeau:** Writing – review & editing, Conceptualization. **Janita Jossie Botha:** Writing – review & editing, Conceptualization. **Giada Luraschi:** Writing – original draft. **Joanne Hort:** Writing – review & editing, Conceptualization. **Luisa Torri:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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Data availability

No data was used for the research described in the article.

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