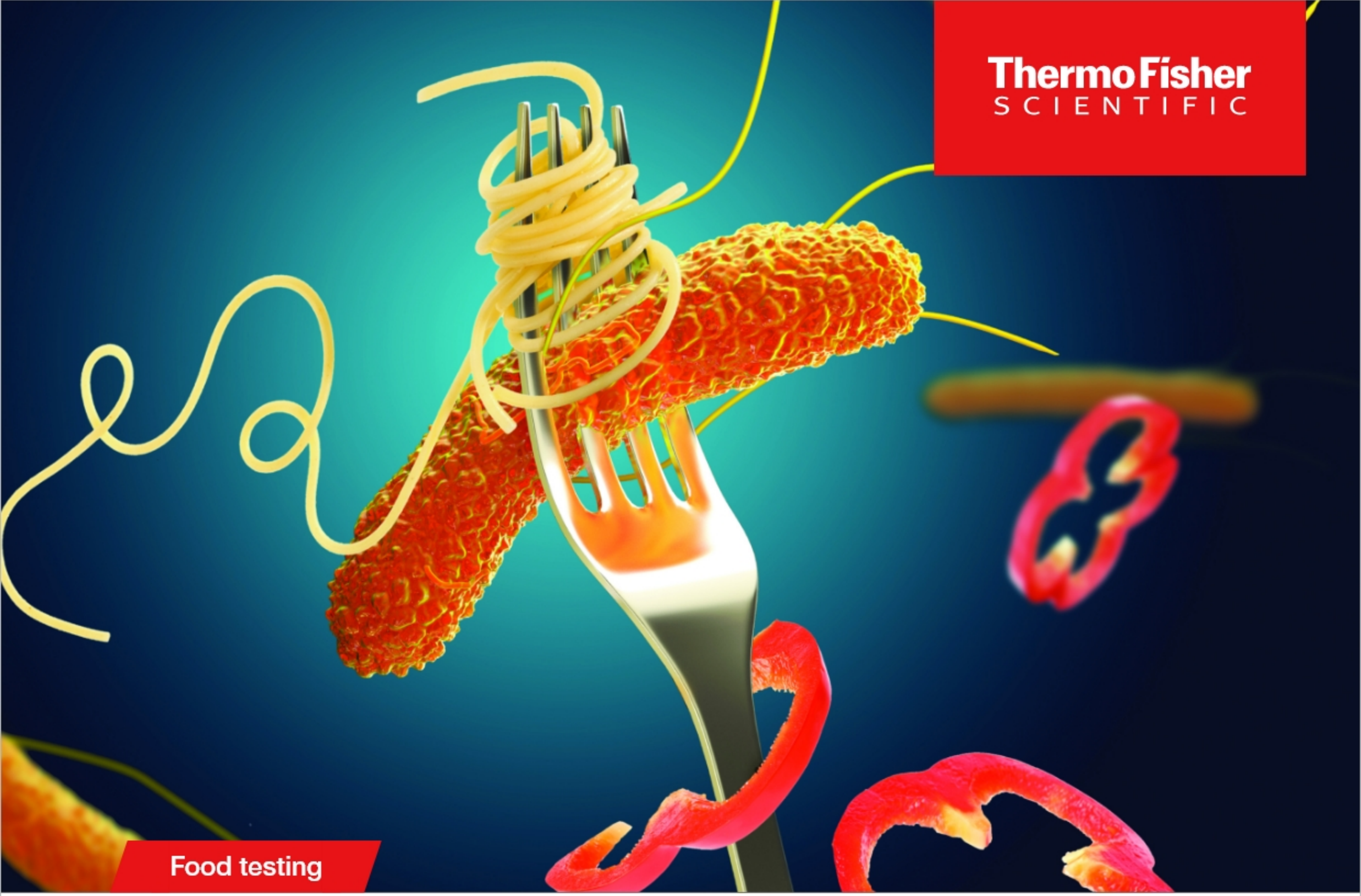

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ADVANCES IN SENSORY SCIENCE: FROM PERCEPTIONS TO CONSUMER ACEPTANCE

Emotional responses to taste and smell stimuli: Self-reports, physiological measures, and a potential role for individual and genetic factors

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Abstract

Taste and olfaction elicit conscious feelings by direct connection with the neural circuits of emotions that affects physiological responses in the body (e.g., heart rate and skin conductance). While sensory attributes are strong determinants of food liking, other factors such as emotional reactions to foods may be better predictors of consumer choices even for products that are equally-liked. Thus, important insights can be gained for understanding the full spectrum of emotional reactions to foods that inform the activities of product developers and marketers, eating psychologist and nutritionists, and policy makers. Today, self-reported questionnaires and physiological measures are the most common tools applied to study variations in emotional perception. The present review discusses these methodological approaches, underlining their different strengths and weaknesses. We also discuss a small, emerging literature suggesting that individual differences and genetic variations in taste and smell perception, like the genetic ability to perceive the bitter compound PROP, may also play a role in emotional reactions to aromas and foods.

KEYWORDS
aroma, flavor, taste

1 | INTRODUCTION

Emotions are commonly defined as fast alterations of affective state due to rewarding or punishing stimuli. They are coordinated with changes in facial expression, physiological status and endocrine responses (LeDoux, 1998; Kadohisa, 2013; Rolls, 2005). These changes have the evolutionary purpose of preparing the body to respond to the external environment to both ensure survival and maintain health (Matsumoto & Ekman, 2009; Nesse, 1990). There is little agreement on how many emotions can be distinguished within the human repertoire. According to Ekman's Discrete Emotion Theory, there are six basic emotions that correspond to a well-defined profile of physiological and behavioral responses, which are primitive and universally recognized, for example, happiness, surprise, fear, anger, sadness, and disgust. By contrast, complex emotions such as grief and pride are a result of a mixture between basic emotions (Ekman, 1999; Ekman et al., 1987). One popular view (Barrett & Russell, 1998) maintains that all emotions exist within a framework described by two dimensions: valence (pleasure vs. displeasure) and arousal (degree of activation). However, Barrett (2017) suggested that the ability to distinguish one emotion from another was based solely on physiological response patterns.

Over the past few decades, there has been increasing interest in understanding emotional reactions to the taste and flavor of foods and how these experiences drive product choices and eating behavior. For instance, familiar foods (e.g., chocolate and pizza), often referred to as "comfort foods," are widely known to elicit feel-good sensations (Parker et al., 2006) and to improve mood (Macht, 2008) even though preferences for specific types of chocolate or pizza vary among individuals. A purchase or consumption decision is often guided by unconscious emotions associated with a product (Lehrer, 2006; Morrin & Tepper, 2021; G. Walsh et al., 2011). Commercial food products that elicit robust emotional reactions may have a competitive advantage in the marketplace compared to similarly-liked products that do not engage consumer emotions (Li et al., 2015). Indeed, food choices may be motivated more by their emotional impact than by their pleasantness (Cardello et al., 2012; Jaeger & Hedderley, 2013; King et al., 2010, 2013; Ng et al., 2013). Individual differences in the reward value of foods may also have important downstream implications for nutrition and health. For example, obesity may be associated with higher emotional reward from food aromas and flavors, and depression may arise in individuals with disruptions in sensitivity to reward or punishment systems (Rolls, 2019a, 2019b).

Emotions can be studied in a variety of ways. The major methodological approaches generally fall into two categories, self-reported (survey) methods and implicit (nonverbal) methods that primarily rely on physiological measurement. These methods have different strengths and weaknesses, and some methods may be more applicable or feasible than others for understanding food emotions in a specific context. The goal of this review is to help sensory and consumer scientists, nutritionists, psychologists, food scientists, product developers, and marketers to better understand why measuring emotions may be important in food research and to provide examples of how emotions are measured and some commentary on the value of these measures in understanding consumer behavior.

This review starts with a brief overview of the taste and smell systems and their involvement in the central processing of emotional responses. We review and critique major questionnaire methods, the use of pictorial methods including emoji, as well as physiological methods such as heart rate variability, skin conductance, and eye tracking. Individual differences in aroma/flavor familiarity, culture, and genetics are also important determinants of emotional responses to foods and are woven into our discussion. A unique focus of this review is on the role of genetic variability in taste and smell as a potential mediator of emotional responses, an area that has only recently gained attention in food research. This review is written with the nonexpert in mind. Readers seeking a deeper discussion of emotions and their measurement are referred to the comprehensive reviews on this topic by (Low et al., 2022; Prescott, 2017), the volume by (Meiselman, 2021a) and a recent collection of editorials and commentaries (Meiselman, 2021b).

2 | CHEMICAL SENSES OVERVIEW

2.1 | Taste system

The human senses function as a conduit between the environment and consciousness by interacting with external stimuli and sending information to the brain. Among all the senses, the rewarding or the punishing value of foods are primarily determined by olfaction and taste (De Araujo et al., 2003). Taste discriminates harmful compounds from nutritious food. This ability allows us to avoid ingesting toxic substances or spoiled food that are perceived as bitter and sour, respectively, and favors the acceptance of sweet compounds like glucose, that represent a source of energy (Chaudhari & Roper, 2010). The distinction between toxic and nutrient-containing food was an evolutionary essential when humans had to choose from a broad variety of natural food sources in the environment. As noted by Scott (2005), the gustatory system serves as the "final arbiter" for food ingestion or rejection (Scott, 2005).

There is a broad agreement that there are five types of basic tastes (sweet, salty, sour, bitter, and umami) that can be detected by humans. Numerous studies also include free fatty acids (released through the breakdown of dietary fats in the mouth) on the list of basic tastes (Ebba et al., 2012; Mattes, 2009, 2010; Pepino et al., 2012).

The taste apparatus consists of individual taste cells organized into taste buds which are modified epidermal cells located in sensory units in the surface layers of the tongue. Taste molecules dissolved in saliva access taste cells via the taste pore, an opening on the apical surface of the taste bud. Every taste cell codes for one specific taste receptor type which is located in the microvilli surrounding the taste pore. Taste buds are organized into taste papillae which hold and orient the taste buds towards the saliva (Figure 1). In humans, three classes of papillae are associated with taste function (fungiform, foliate, and circumvallate); the fourth type (filiform) is associated with tactile sensations (Miles et al., 2018, 2022).

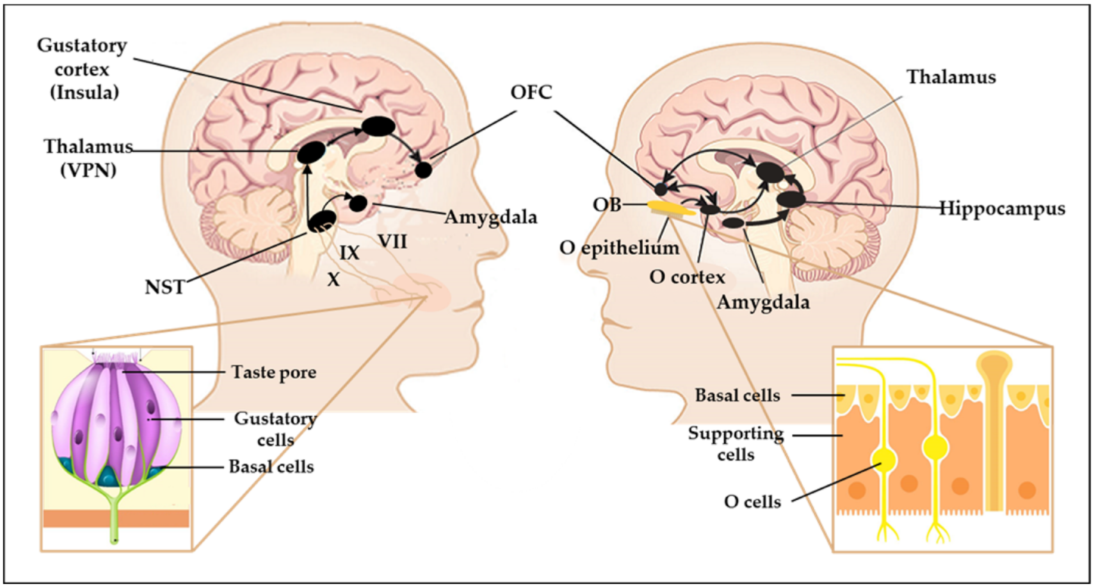

FIGURE 1 Summary of the peripheral structures and the central pathways involved in taste (left) and olfaction (right) perception. Figure adapted from Figure 1. in Melis et al. (2021) *Abbreviations*: NST, nucleus of solitary tract; O, olfactory; OB, olfactory bulb; OFC, olfactory cortex; VPN, ventral posteromedial nucleus; VII, IX, and X, cranial nerves

When a stimulus reacts with a specific taste receptor, the base of the cell body activates the associated nerve fibers (Nagai et al., 1996). Three cranial nerves (chorda tympani, glossopharyngeal, and vagus) carry taste information to the Nucleus of the Solitary Tract (NTS) located in the Medulla. Second-order taste neurons from the Medulla ascend to the Ventral Posteromedial Nucleus of the Thalamus. From here, third-order fibers synapse in the insular cortex and frontal operculum, collectively known as the primary taste cortex, which detect the intensity and identity of the taste stimulus. Gustatory information from the NTS also travels to the amygdala and the hypothalamus where the hunger/satiety center is located. This input modulates the hunger/satiety center, and emotional and physiological response related to food (Hadley et al., 2004; Shipley & Reyes, 1991).

2.2 | Olfactory system

The sense of smell has several functions. It warns us about the presence of toxic volatiles in the environment and guards against the consumption of spoiled or harmful foods. The observation that unpleasant odors are perceived faster than pleasant ones emphasizes the critical role of olfactory cues in a rapid-response system to harmful stimuli (Bensafi, Rouby, Farget, Vigouroux, et al., 2002). Olfaction is also a major contributor to the flavor of food. Indeed, olfactory signals carried through the nose make up the preponderance of cues that consumers popularly refer to as “food flavor” (Murphy et al., 1977; Santos et al., 2004). Thus, flavor is an integral part of food recognition, helping us gauge whether a food is suitable to eat and its potential for providing hedonic pleasure and enjoyment.

Olfactory receptors are located in the olfactory epithelium in the roof of the nasal cavity (Figure 1). Volatile compounds reach the olfactory epithelium by orthonasal stimulation (smelling through the nose), and via the retronasal pathway (Pierce & Halpern, 1996) when a food is taken into the mouth, chewed, and swallowed. Stimulation of olfactory receptors by volatile compounds converts the chemical information to an electrical impulse that is conveyed to specific regions of the olfactory bulbs (OB) called glomeruli. Mitral cells in the OB combine the impulses from glomeruli and send them to the primary olfactory (or piriform) cortex, where the intensity and identity of odors is represented. Olfaction is the only sensory signal that does not make a direct connection with the thalamus. Instead, mitral cells project their axons to the cortex, resulting in a faster activation than that evoked by other sensory modalities (Gottfried, 2006). From the olfactory cortex, impulses are sent to the orbitofrontal cortex (OFC) for further processing. The amygdala maintains close networks with primary olfactory areas. Indeed, among the stimuli from all sensory modalities that activate this area, amygdala nuclei respond more quickly to odor stimuli (McDonald, 1998).

3 | CENTRAL PROCESSING OF EMOTIONS

Taste and olfaction both converge in the OFC where flavor (the conscious sensation of a food made by its taste, olfaction, and texture stimuli) is formed by neural association of the inputs. De Araujo et al. (2003), using fMRI methodology, showed that olfactory and taste inputs are integrated also in the amygdala and insular cortex. However, some authors showed that the interaction between taste and orthonasal olfaction can happen at all levels of the pathway (Small, 2012). Thanks to its anatomical connection with the sensory pathways and the physiological regulations centers, the amygdala plays a key role in processing (Gottfried et al., 2003; Murray & Izquierdo, 2007) and detecting the intensity of emotions (Bonnet et al., 2015), due to the inputs it receives from the thalamus (subcortical route) and the neocortical sensory areas (cortical route) (LeDoux, 1989, 1998; Gainotti, 2020; Kadohisa, 2013). Differential response patterns in the amygdala for pleasant versus unpleasant stimuli, map with rapid encoding for unpleasant odors (J. Jin et al., 2015). Together with the amygdala, other brain structures like hypothalamus and prefrontal cortex are associated with cognitive processes, those same areas where olfactory and gustatory inputs are sent for hunger/satiety modulation.

3.1 | Emotional experiences

As stated previously, the chemical senses are closely linked to positive and negative emotions. For example, sweet taste has been linked to pleasantness, with the highest valence and arousal ratings, while bitter taste corresponded to anger and disgust; mixed emotions are evoked by salty and sour taste (Robin et al., 2003; Wang et al., 2016). In the realm of olfaction, the fragrance of vanilla and lavender evoked more robust romantic and warm emotions compared to other equally-liked fragrances (Rétiveau et al., 2004). On the other hand, olfactory memories for certain fruits and vegetables (except onion/garlic) and pastries were commonly associated with positive emotions, while burnt and deteriorated food, smoke and chemicals were related to negative emotions in surveys of German and Japanese consumers (Schleidt et al., 1988).

Likewise, food consumption and eating behavior of humans are influenced by emotional and affective responses to food. In one study, Desmet and Schifferstein (2008) showed that positive emotions (satisfaction, pleasure, and enjoyment) were more often associated with tasting or eating everyday foods than negative emotions. This imbalance (often described as hedonic asymmetry) may reflect the fact that we generally choose to eat foods that we find pleasant and rewarding and tend to avoid foods we dislike. Thus, the relationship between foods and emotions are strongly linked to memories and pleasures derived from eating those foods in the past (Thomson et al., 2010). These strong bonds between reward and emotions drive appetite and eating (Rolls, 2015), underlining the mutual relationship between positive emotion and overall product acceptability (Desmet & Schifferstein, 2008; King & Meiselman, 2010; King et al., 2010; Thomson et al., 2010).

Unavoidably, when we encounter a food that we recognize from past experiences, we have already formed memories and opinions about that food that can alter its emotional impact (Thomson et al., 2010). Finally, although vision and hearing also participate in food identification, taste, and olfaction in concert act as the most critical and final checkpoint for food acceptance or rejection (Scott, 2005).

4 | SELF-REPORTED MEASUREMENT

Measuring an individual's subjective emotional experiences from sensory stimuli, regardless of their source, can be highly challenging, and a variety of surveys and questionnaires have been developed over the years to address the specific goals of aroma and flavor research. Self-reported methods can be broadly divided into verbal and visual (including pictorial) techniques which are reviewed in the following sections.

4.1 | Verbal self-reported tests

Self-reported questionnaires are generally composed of a list of emotion words from which consumers select the verbal descriptors which match how they feel following exposure to a taste or aroma stimulus or food or beverage product. These questionnaires can differ in both the nature and number of words provided.

4.1.1 | Geneva Emotion and Odor Scale (GEOS) and its derivatives

Chrea et al. (2009) developed the Geneva Emotion and Odor Scale (GEOS) to assess emotional responses to both food and nonfood odors. Starting with a list of 480 terms extracted from the literature, subjects rated the relevance of each term for describing an experienced emotion. The large number of terms was then reduced using confirmatory factor analysis to group the terms into six emotional factors where each factor was characterized by a subset of related terms, for example energizing refreshing, soothing peacefulness (Chrea et al., 2009). A second group of subjects utilized an emotional intensity scale ("none at all" to "very intense") to rate the emotional impact of

56 edible/nonedible odors differing in pleasantness and familiarity. In a comparison study, emotions evoked by everyday odors were better discriminated using GEOS's six categories, which collects a more complete spectrum of emotions, compared to a basic emotions assessment (i.e., anger, fear, and sadness) which is less revealing of an individual's emotional status. The full GEOS was also superior to the tridimensional categories approach (activation versus deactivation, pleasure versus displeasure, dominance versus submissiveness) that does not fully characterize the affective effect of different odors (Delplanque et al., 2012).

The GEOS has been used in a cross-cultural context where the same odors were evaluated by consumers in the UK and China and the results compared to those from the first study conducted in Geneva (Switzerland) (Ferdenzi et al., 2011). Importantly, this study showed that emotional terms were used differently across cultures. According to these same authors (Ferdenzi, Delplanque, et al., 2013; Ferdenzi, Roberts, et al., 2013), an emotion lexicon may not reflect the same meaning between different geographic areas or different cultures. These findings are consistent with earlier cross-cultural studies showing that affective responses to odors varied across geographical regions (Ayabe-Kanamura et al., 1998; Pangborn et al., 1988; Wysocki et al., 1991). In addition, lexicons containing long lists of emotional terms may evoke experimental fatigue in subjects or misunderstanding some of the emotional words may happen (Kenney & Adhikari, 2016).

The ScentMove™ questionnaire was developed as a shortened version of GEOS, adapted for commercial product development needs, where high-volume testing may be necessary. Subjects are requested to express their emotions using only six groups of emotions, each illustrated by three terms. It was validated with a limited set of six strawberry flavors and different floral fragrances in a laboratory environment. The results showed that the strawberry flavors induced divergent emotions even in instances when they were equally liked; the same outcome was observed for fragrances, beverages, and wine aromas (Porcherot et al., 2010, 2013, 2015; Ristic et al., 2019).

Scott et al. (2019) used the GEOS to understand the emotional impact of flavored soups supplemented with spices to increase pungency. Adding chipotle chili pepper to tomato soup decreased ratings of relaxation and increased ratings of disgust and mouthwatering, whereas adding ginger to squash soup did not significantly alter emotional ratings. Despite this imbalance in spice impact, Scott et al. (2019) observed meaningful correlations between specific emotional terms and overall liking for both soups. These results are shown in Figure 2. For the chipotle chili tomato soup, overall liking was positively correlated with well-being and relaxation, and negatively correlated with disgust. Importantly, overall liking of the ginger squash soup was positively correlated with three emotions (well-being, relaxed, and interested). These data suggest that measuring emotions in conjunction with liking may help extract deeper meaning from the latter responses, potentially unmasking underlying and less obvious drivers of liking (Scott et al., 2019).

4.1.2 | EsSense Profile®

While the GEOS has been broadly applied to investigate emotional reactions to pleasant and unpleasant odors, flavors, fragrances and sometimes to food and personal care products, the EsSense Profile® developed by King and Meiselman was specifically designed to address emotions elicited by food (King & Meiselman, 2010; King et al., 2010). The questionnaire consists of 39 descriptors selected to be the most clearly understood as positive, negative or nonclassified emotions related to food. Thirty-five terms are positive and only four are negative reflecting the previously described phenomenon of hedonic asymmetry in which eating is usually viewed as a pleasant experience (Schifferstein & Desmet, 2010). The method uses a check-all-that-apply (CATA) format which is followed by a rate-all-that-apply (RATA), 5-point scale. This allows subjects to choose the emotional terms that are most meaningful to them and then to rate the intensity of those emotions. The RATA approach was more sensitive than CATA for discriminating differences between products in the same category (King et al., 2013).

The EsSense Profile® was validated both within the same product type and across different categories of products including sweet foods like chocolates (Dorado, Pérez-Hugalde, et al., 2016; Piqueras-Fiszman & Jaeger, 2014c; Spinelli et al., 2014) and cakes (Poonnakasem et al., 2016), savory foods like crackers and other snacks (King & Meiselman, 2010; King et al., 2013), dairy products (De Pelsmaeker et al., 2013; Gutjar, de Graaf, et al., 2015; A. M. Walsh et al., 2015; Wardy et al., 2015), fruit and vegetables (Manzocco et al., 2013; Piqueras-Fiszman & Jaeger, 2015; Chonpracha et al., 2020), and beverages like blackcurrant squashes and beer (Chaya, Pacoud, et al., 2015; Ng et al., 2013). It has also been applied in many different research and marketing contexts such as central location, home use tests and internet surveys. These studies showed that the questionnaire effectively discriminated the emotional profiles of products even when they were equally liked. These findings further support the notion that emotional responses to products may be more revealing of their complex impacts on hedonic pleasure, beyond a simple, unidimensional measure of liking (Jaeger, Swaney-Stueve, et al., 2018; King et al., 2010; Ng et al., 2013).

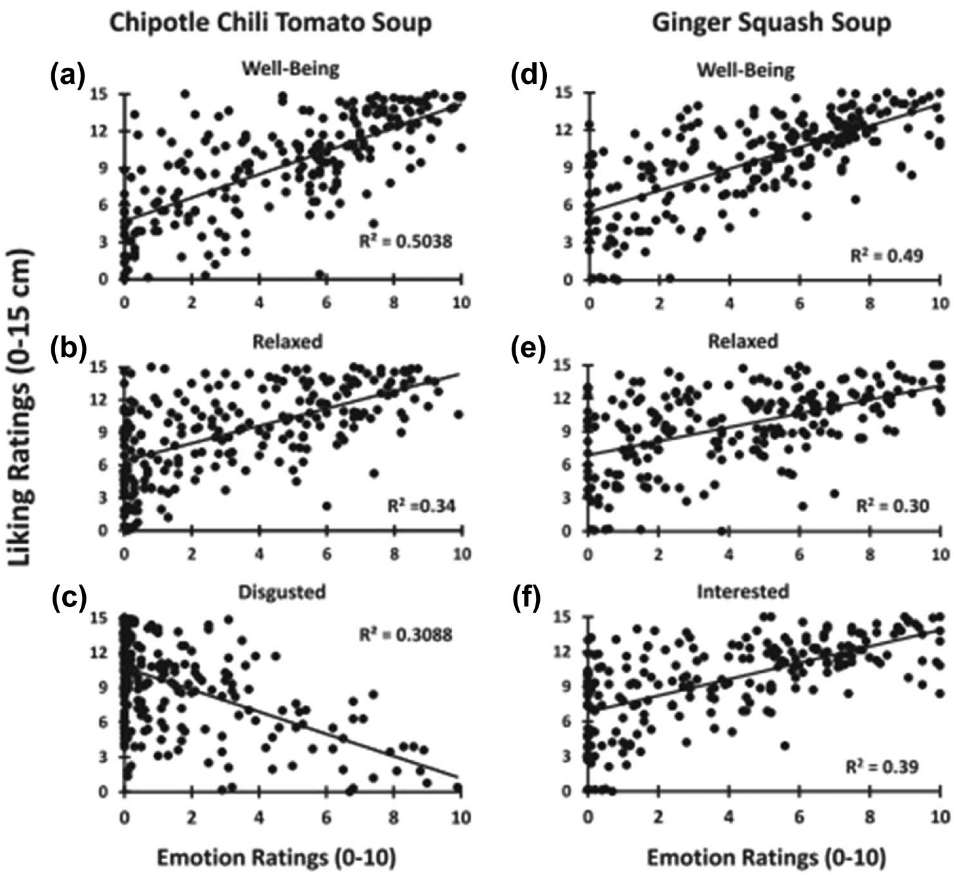

FIGURE 2 Scatterplots and Pearson Correlation coefficients (r) of the relationship between emotions and overall liking of soups. Left panels show overall liking for chipotle chili tomato soup and “wellbeing” (a), “relaxed” (b), and “disgusted” (c). Right panels show overall liking for ginger squash soup and “wellbeing” (d), “relaxed” (e), and “interested” (f). $p < 0.0001$ for all. Data from Scott et al. (2019) with permission

Many approaches have been used to reduce the length of the EsSense Profile® or customize it for specific products. EsSense25 is the shorter version that was developed to facilitate the emotional evaluation of a large number of samples in a product development context (Borgogno et al., 2017; Schouteten, De Steur, et al., 2017). A comparison study showed similarity between the two questionnaires, although with some effects on word meanings due to the reduction in the length of the lexicon (Nestrud et al., 2016). On the other hand, a customized questionnaire may not be discriminative when different types of foods are tested. Future studies should address this issue.

4.1.3 | Emotions and sensory attributes

Schouteten et al. (2015b) developed a method called the EmoSensory® Wheel that combines emotional and sensory terms. The EmoSensory® Wheel was inspired by taste and aroma wheels that are common tools in descriptive analysis to familiarize panelists with sensory attributes. The wheel contains the same number of positive and negative terms and uses a RATA approach wherein a subject selects a term as relevant to the food and then a scale appears for rating the intensity of the term. Their result showed that the questionnaire discriminated products within the same class better than between different classes (Schouteten et al., 2015a, 2015b; Schouteten et al., 2016; Schouteten, Gellynck, et al., 2017; Oliveira et al., 2020). Additionally, when using the EmoSensory® Wheel before and after consuming four cheeses, consumers expressed more negative emotions to samples of cheese labeled as low-salt and low-fat than to cheese samples without nutrient content labels, which were perceived to have a higher overall expected liking (Schouteten et al., 2015a).

Finally, Cardello et al. (2016) developed and validated the circumplex emotion model, which consists of 12 domains of emotion organized into two dimensions of pleasure and arousal that are arranged in a circular space (Cardello et al., 2016; Jaeger, Cardello, Chheang, et al., 2017; Jaeger, Cardello, Jin, et al., 2017; Jaeger, Spinelli, et al., 2018; Jaeger, Xia, et al., 2019). This single-response questionnaire was inspired by the bidimensional representation of cognitive human affect (Russell, 1980) and sufficiently discriminated between a multitude of stimuli, even in different cultures (Jaeger et al., 2020).

4.1.4 | Consumer-led lexicon questionnaires

The self-reported questionnaires described above with a predefined lexicon were developed for a wide range of products. However, the list of emotions might contain elements with little or no relevance for some product categories, or they might not list some relevant emotions for a specific type of product (Jaeger, Cardello, et al., 2013). A product-specific questionnaire could help to better capture emotions elicited within a product category (Ng et al., 2013; Spinelli et al., 2014, 2015). The workflow to develop a consumer-led lexicon starts with a list of emotion terms generated by consumers (Bhumiratana et al., 2014) or by searching the literature (Ferrarini et al., 2010). It is then filtered to remove synonyms or redundant terms, and finally tested for accuracy. Some authors grouped the terms into categories to decrease subjects' fatigue (Chaya, Eaton, et al., 2015; Eaton et al., 2019; Mora et al., 2019). Consumer-led questionnaires have been developed for dark chocolate (Thomson et al., 2010), wine (Ferrarini et al., 2010), blackcurrant squashes (Ng et al., 2013), chocolate and hazelnut spreads (Spinelli et al., 2014), coffee (Bhumiratana et al., 2014), strawberries, and beer (Chaya, Eaton, et al., 2015; Dorado, Chaya, et al., 2016; Eaton et al., 2019).

By nature, consumer-led lexicons are language and culture specific, although they are often translated and adapted for use in another population. Nevertheless, even when populations speak the same language, cultural differences can play a substantive role in how the lexicon is used. A cross-cultural study on alcoholic beverages showed larger differences in emotional reactions among participants who spoke the same language but came from different cultures. This was observed among English-speaking participants living in different countries (United States, United Kingdom, Australia, and New Zealand) and Spanish-speaking individuals living in Spain and Mexico (van Zyl & Meiselman, 2015). This emphasizes the importance of choosing a validated questionnaire that is both validated for the language, but also for the culture.

4.2 | Visual self-reported tests

Visual self-reported measures can simplify experimental procedures by using schematic faces, like the visual analog mood Scale (Stern et al., 1997) or by replacing words with pictures of facial and body expressions. This type of approach can be valuable in multicultural studies and investigations in children. For example, the Product Emotion Measurement Instrument (PrEmo®) assesses product emotions using a set of seven positive and seven negative cartoon animations instead of words (Desmet et al., 2000). While PrEmo® was not developed for a food purpose, it differentiated emotions elicited by seven breakfast drinks despite its limited number of emotional descriptors (Gutjar, Dalenberg, et al., 2015; Gutjar, de Graaf, et al., 2015). In general, nonverbal measures solve problems that can arise in translating a lexicon to other languages where emotional words may not have the same meaning.

Another popular alternative for the emotional evaluation of food and beverage products is the use of facial emoji. Vidal et al. (2016) developed a list of positive and negative emoji by choosing the most common ones used for describing food on Twitter (Vidal et al., 2016). Although emoji-based responses may be subject to multiple interpretations based on familiarity, as well as socio-demographic and behavioral factors, Jaeger and Ares (2017) showed that emoji were effective in eliciting food-related emotions, despite cultural differences (Jaeger & Ares, 2017); the participants also viewed the method as less boring (Ares & Jaeger, 2017). Emoji have also been used successfully in studies with preadolescents in a variety of experimental contexts (laboratory and online surveys) (Gallo et al., 2017b; Jaeger, Lee, et al., 2017; Jaeger, Vidal, et al., 2017; Jaeger, Lee & Ares, 2018; Jaeger, Lee, Kim, et al., 2018; Jaeger, Roigard, et al., 2018; Jaeger, Xia, et al., 2018; Schouteten et al., 2018; Jaeger, Roigard, et al., 2019; Lima et al., 2019; Sick et al., 2020; Vidal et al., 2020). Previous studies in children have shown a high positive correlation between emotional responses and liked foods (Gallo et al., 2017a; Swaney-Stueve et al., 2018). Although the strengths of emoji-based questionnaires are their ecological validity, familiarity, and shared meanings in different cultures (Jaeger et al., 2021), studies are needed to address the internal validity of these visual self-reported questionnaires.

Two additional nonverbal techniques warrant attention: the Mood Portrait and the Mood Signature approach. A unique feature of these two techniques is that subjects assign an emotion to the stimulus rather than evaluating how the stimulus makes them feel. In the Mood Portrait approach, subjects chose from a library of emotional photographs that best matched exemplars of commercial fragrance odor types (Churchill & Behan, 2010). The Mood Signature Questionnaire developed by Jin et al. (2018) provides a list of nine mood descriptors and subjects select the mood that best (or mostly) describes an odor. Presumably, both techniques reduce report bias by shifting the focus from the subject's own internal emotional state to the stimulus, thereby lowering the cognitive demand on subjects to interpret their own feelings and to state them verbally.

Using the Mood Signature Questionnaire, Jin et al. (2018) found that pleasant aromas generally evoked positive emotions, and changes in stimulus intensity altered the emotional valence of some of them. These effects are illustrated in Figure 3, showing selection frequencies of the "mostly" mood terms for positive and negative emotions after subjects were exposed to three pungent single-component odors, presented at low and mid-range concentration. At low concentrations, the aromas of cinnamaldehyde, methyl cinnamate, and geraniol were characterized by calm-relaxed mood that shifted to exiting-energized mood at mid-range concentrations. The moods of three other compounds that were rated lower in pungency (citral, citronellol, and phenyl ethyl alcohol [PEA]) did not change with stimulus concentration (data not shown). In a second study, Gaby and Tepper (2020) showed that citral odor evoked mostly excited-energized mood, while nonalactone (coconut) and vanillin elicited calm-relaxed mood. These findings are consistent with earlier studies examining the effects of ambient odors on mood and performance. For example, citrus aromas and peppermint have been associated with excitement and vigor (Baccarani et al., 2020; Herz et al., 2004; Raudenbush et al., 2002), whereas lavender aroma elicits calm and peacefulness (Herz, 2009; McCaffrey et al., 2009).

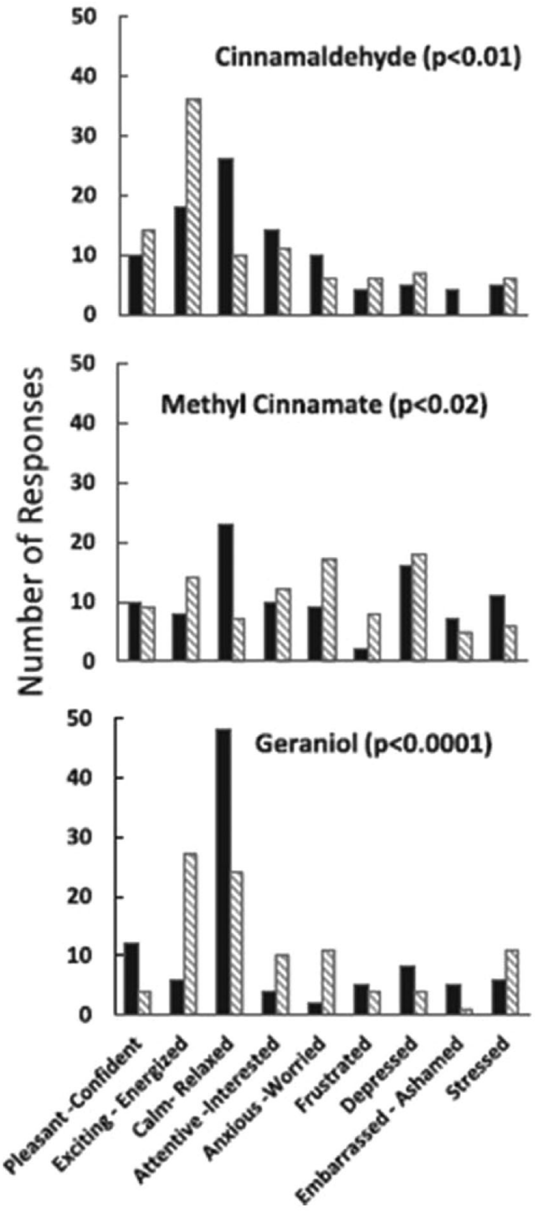

FIGURE 3 Selection frequencies of the "mostly" mood terms from the Mood Signature Questionnaire for aroma compounds at low concentrations (black bars) and mid-range concentrations (stripped bars). The height of each bar represents the number of participants who selected each term as the best descriptor for the mood of the aroma. The mood signature of cinnamaldehyde, geraniol, and methyl cinnamate shifted from calm-relaxed at low concentrations to exciting-energized at mid-range concentrations (p range = 0.0001–0.02 by Chi-square analysis). Data from Jin et al. (2018) with permission

4.3 | Summary: Self-reported measures

Self-reported questionnaires are quick to administer, user-friendly, and the data they generate are easy to process (Cardello & Jaeger, 2021). Generally speaking, current methods effectively discriminate one odor stimulus from another, and can differentiate emotions from products in the same class or across different product classes. However, all self-reported methods have their strengths and limitations, and no single method can be considered universally suitable and appropriate for all applications. In choosing which method to use, operators should carefully consider the characteristics of the stimuli under study or if a consumer-led lexicon has already been developed for the product category under study. The characteristics of the subject population should be considered as participants may vary in their ability to conceptualize, identify, and verbalize perceived emotions. In the case of research with children, pictorial and emoji-based methods would be preferred. Although cognitive biases cannot be eliminated, recognizing that they may be present in the data encourages critical evaluation and sound interpretation of the results. Finally, self-reported emotions are generally retrospective in nature in that subjects are asked to describe their emotions after sample exposure. This is in contrast to physiological responses (described in the next section), which are immediate and concurrent with the stimulus. Selected examples of recent studies relying on questionnaires for assessing emotional responses to odor stimuli and foods and beverages can be found in Table S1 and S2, respectively.

5 | PHYSIOLOGICAL MEASURES

Physiological (or implicit) measures are those that do not depend on a subject's ability to recognize, interpret, and verbalize their internal affective state. Since implicit measures such as analysis of brain activity, autonomic nervous system function, and facial expressions are based on automatic processes according to appraisal theory (Moors et al., 2013; Roseman & Smith, 2001), they are considered unbiased reflections of our internal physiological state. The next sections discuss the major types of physiological measures and their strengths and weaknesses as predictors of emotional reactions.

5.1 | Central measures

During the last two decades, functional magnetic resonance imaging (fMRI) has been frequently used to investigate odor valence and hedonic responses by assessing specific patterns of neural activity in cerebral cortex. Numerous studies have shown that unpleasant odors elicited higher and more rapid neural responses than pleasant ones in piriform cortex (Anderson et al., 2003; Bensafi et al., 2007; Gottfried et al., 2002), in amygdala (Anderson et al., 2003; Royet et al., 2003), and OFC (Anderson et al., 2003; De Araujo et al., 2005; Rolls & Scott, 2003). This topic has been recently reviewed by Mantel et al. (2019). fMRI has also been used to investigate the correlation between brain activity and perceived pleasantness elicited by the in-mouth flavor of liquid food stimuli (tomato soup and chocolate milk), demonstrating that the activity in OFC was higher if the food was perceived as pleasant (Kringelbach et al., 2003).

A critical question in the field is whether neuroimaging studies can map specific areas of the brain where singular emotions are perceived. This seems unlikely, however, as individual neurons or neural pathways dedicated to specific emotions have yet to be identified (Lindquist & Barrett, 2012; Touroutoglou et al., 2015). Despite this, some fMRI studies reported a valence-specific pattern of brain activation associated with overall emotional regulation (Anders et al., 2004; Dolcos et al., 2004). For example, Anders et al. (2004) investigated whether subcortical and higher cortical structures are activated by nonfood pictures which largely varied in valence and arousal. This study revealed positive correlations between the self-reported valence of emotions and activity in the amygdala and insular cortex. Even though fMRI recordings do not fully capture the rich complexity of emotional experiences, they can nevertheless provide some limited insights for understanding consumer emotional experiences.

5.2 | Autonomic nervous system measures

It is well known that emotional states can induce extremely fast autonomic nervous system (ANS) responses. The ANS regulates autonomic bodily responses via the sympathetic and parasympathetic branches that work in concert to maintain bodily homeostasis. Specifically, during food consumption, the ANS controls saliva release to prepare for food ingestion and swallowing. The ANS also increases gastric motility and intestinal secretions, and directs greater blood flow to the gastrointestinal system (McCorry, 2007). The idea that specific emotions may be associated with particular ANS pathways is consistent with an evolutionary model explaining how the body rapidly responds to physical and psychological threats with expressions of surprise, fear, anger, and so forth (Levenson, 2014). Whether everyday taste and smell experiences are capable of eliciting emotion-specific ANS responses remains an open question.

The most representative indices of ANS activation are cardiovascular and electrodermal responses. In a comprehensive review of the ANS exploring emotional responses, Kreibig (2010) showed that Heart Rate (HR), Respiratory Frequency (RF) and Skin Conductance Level (SCL) were the most utilized methods respectively among cardiovascular, respiratory and electrodermal measures (Kreibig, 2010). Rousmans et al. (2000) recorded ANS responses while subjects perceived sweet, sour, bitter and salty tastes, and showed that changes related to sweet taste were weaker that those induced by sodium chloride, citric acid and quinine. In particular, quinine showed the largest change especially in HR variation. This same team found no correlation between hedonic ratings and changes in ANS for different pleasant sweet stimuli (Leterme et al., 2008). Thus, an unpleasant taste exemplified by bitter quinine produced greater HR variability than pleasant ones. This same dichotomy has been observed in olfaction where HR variability increased more with unpleasant odors, than with pleasant ones (Alaoui-Ismaili, Robin, et al., 1997; Alaoui-Ismaili, Vernet-Maury, et al., 1997; Bensafi, Rouby, Farget, Vigouroux, et al., 2002; He et al., 2014).

Muroni et al. (2011) studied the interval between two R waves (RR) in a constant electrocardiogram recording (known as the cardiac circle). They showed that taste stimuli perceived as pleasant and unpleasant, produced bradycardia and tachycardia, respectively, both in women and men. As shown in Figure 4, RR intervals were shorter

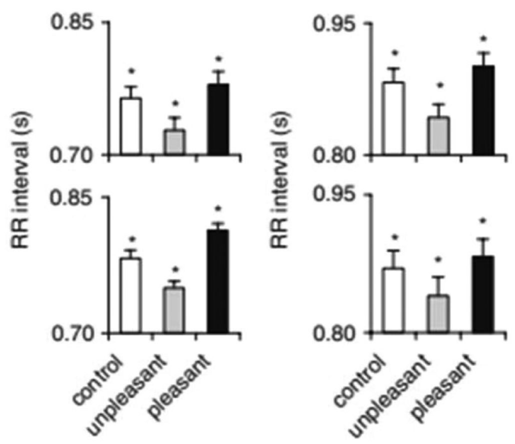

FIGURE 4 Mean values ± SEM of RR intervals of the cardiac cycles following each flavor stimulation measured in women (left graphs) and in men (right graphs) in the first test session (upper graphs) and in the second test session (lower graphs). Experiments were repeated on the same volunteers after a month's period to confirm the results obtained in the first test session. *Significant difference ($p \leq 0.0027$, post hoc Tukey test subsequent to three-way ANOVA). Data from Muroni et al. (2011) with permission

for unpleasant odors compared to control, whereas RR intervals were longer for pleasant ones (also relative to control). In the same study, HR variation was used to show that negative emotions produced increased sympathetic activity, whereas positive emotions increased vagal activity. This increase in vagal activity might represent a preparatory signal for ingestion and digestion of pleasant food (Muroni et al., 2011).

Measurement of respiration and skin conductance together may provide additional information on ANS functioning with respect to emotions. In one study, RF changed in response to unpleasant stimuli associated with disgust, as well as with increased expiration and decreased inspiration. These changes were not associated with the ability to discriminate the odorants (Alaoui-Ismaili, Robin, et al., 1997). Many studies have shown that odor experiences are positively correlated with SCL, which is directly influenced by the eccrine sweat glands and is controlled only by the sympathetic branch of the ANS. Nevertheless, these changes in skin conductance amplitudes and response times to pleasant and unpleasant stimuli do not appear to be emotion-specific (Alaoui-Ismaili, Robin, et al., 1997; Bensafi, Rouby, et al., 2002a, 2002b; Bensafi, Rouby, Farget, Vigouroux, et al., 2002; Delplanque et al., 2008; Delplanque et al., 2009; Heuberger et al., 2001), but rather, tied to arousal levels. For example, Fredrikson et al. (1998) showed decreased electrodermal activity in response to low arousal emotions (sadness and relief) that might indicate a decrease in motor activity associated with those emotions.

The effects of odor stimuli that also elicit trigeminal responses (i.e., nasal pungency) have been widely unexplored in studies on emotions. Nevertheless, two studies conducted by Gerard Brand and Jacquot (2001, 2002) showed higher skin conductance amplitude after an irritating odor (allyl isothiocyanate) as compared to a nonirritating one (phenylethanol) (Brand & Jacquot, 2001, 2002). More studies need to be conducted on physiological measures associated with pungent stimuli to better understand how this class of stimuli affects emotions.

Despite the argument made by some authors that emotional experiences can only be linked with nonspecific patterns of ANS activation (Barrett, 2006; Cannon, 1927), other researchers demonstrated at least partial differentiation of emotional responses when using multiple physiological measures together (Schwartz et al., 1981; Bloch et al., 1987; Collet et al., 1997; Ekman et al., 1983; Lang et al., 1980). Specifically, Ekman et al. (1983) were able to distinguish anger from fear and sadness when both HR and skin temperature measures were high. According to Collet et al. (1997), the results of electrodermal, thermal, and respiratory recordings differentiated the six basic emotions when the results were compared two-by-two. Nevertheless, other studies have shown that ANS measures are better indicators of arousal state than valence. This is revealed in studies showing that skin conductance is positively correlated with subjective ratings of arousal and independent of stimulus valence (Bradley & Lang, 2000; Cacioppo et al., 2000).

There are a number of practical limitations when measuring physiological responses to aroma, flavor, and taste stimuli. One of the biggest challenges is that the physical act of sipping a fluid sample or chewing and swallowing a semi-solid or solid food interferes with physiological recordings. This is why physiological measures are mainly used in laboratory studies with simple stimuli and model systems that do not represent the complex real-life conditions of product tasting.

Another critical issue is the subjectivity of self-reported sensory ratings, the most common method for collecting taste and smell responses in human studies. Subjective biases are well known in sensory testing and can arise from a multitude of factors including preconceived ideas about the samples, decreased motivation/attention to the rating task especially with large sample sets, and central tendency (i.e., the propensity to avoid using the ends of the rating scale) (Meilgaard et al., 2015). Various experimental design strategies are used to control these psychological errors, but they cannot be completely eliminated.

The ability to establish robust associations between self-reported intensity ratings and more reliable ANS data could be undermined by the subjective nature of the sensory ratings. A novel method for measuring electrophysiological recordings from the human tongue

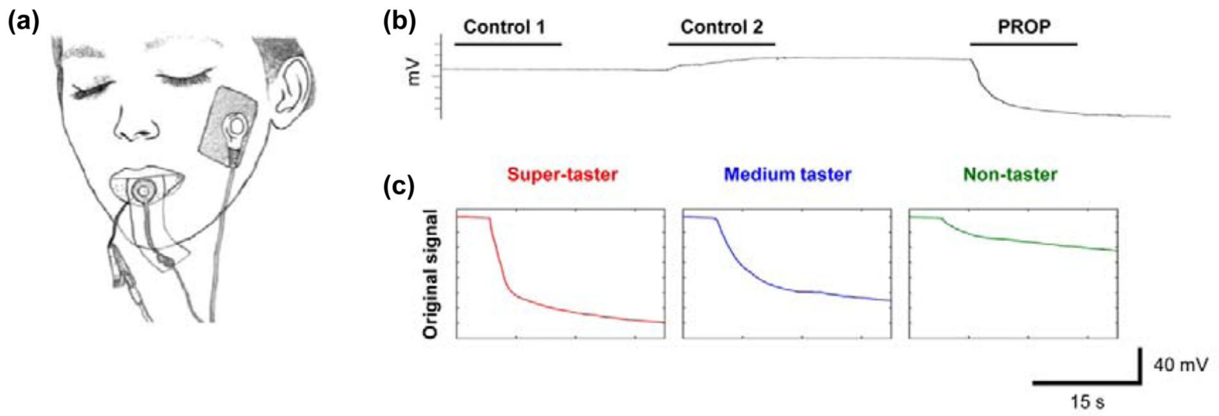

FIGURE 5 (a) Drawing showing how electrodes are positioned for differential electrophysiological recordings. A silver electrode is placed on the ventral surface of the tongue. A second electrode with a circular hole on the middle for application of the taste stimulus is placed on the dorsal surface. A third disposable adhesive electrode (the ground terminal) is placed on the skin of the subject's left cheek. (b) Example of a response to a sequence of three stimulations (15 s): a paper disk (control 1), a paper disk impregnated with 30 μl of spring water (control 2), and a paper disk impregnated with 30 μl of PROP solution. (c) The bio-electrical responses to stimulation with PROP from three individuals who perceive different intensities from PROP (i.e., a representative PROP super-taster, a medium taster, and a nontaster). More details on genetic differences in PROP tasting is presented in Section 7, below. Data from Sollai et al. (2017) with permission

can overcome this problem for basic taste evaluations. This technique has been used to rapidly measure variabilities in the bitter tasting compound PROP (6-n-propylthiouracil) in a manner that avoids reporting bias and reveals robust, physiologically derived differences in individual perceptual experiences (Sollai et al., 2017). Figure 5 shows a drawing of the electrode placement for this system and examples of bioelectrical signals recorded from subjects following stimulation with PROP. As will be described in more detail in Section 7.0, individuals can be classified as PROP nontasters, medium tasters, and super-tasters based on their subjective ratings of PROP bitterness. As shown in Figure 5, when PROP was applied directly to the tongue, the amplitude of the electrophysiological response was highly consistent with these groupings, that is, amplitudes were highest in super-tasters and lowest in non-tasters.

Studies using this recording method have reported high correlations between amplitude of signals, perceived intensity, number of fungiform papillae on the anterior tongue, and *TAS2R38* genotype (the gene controlling PROP tasting). Together, these findings demonstrate that the method directly and effectively measures the degree of activation of peripheral taste function (Sollai et al., 2017). In more recent studies, the method was tested for all basic taste stimuli (i.e., sweet, sour, salty, bitter, umami, and fatty acid) (Sollai, Melis, Mastinu, et al., 2019; Melis et al., 2020). If combined with ANS recording or other physiological measurements, this technique has the potential to reveal new insights for understanding the complex relationships between peripheral perception of tastes and elicited emotions. For example, more complex stimuli such as flavored solutions or fruit-flavored beverages could be applied directly to the tongue to assess how changes in sweetness concentration alter peripheral taste function. This information could be linked with subjective ratings and ANS responses. These experiments are technically difficult to conduct but might provide complementary information and perhaps a more complete picture of the impact of sweetness changes on emotional expression.

5.3 | Facial expressions as measures of emotion

All major theories of emotion support the idea that bodily reactions reflect emotional status and that measurement of specific physiological changes are useful tools to understand and categorize emotion responses. As discussed in the previous section, analytical approaches may be more effective compared to conscious methods, such as self-reports because the latter are highly influenced by cognitive bias that may overshadow genuine perceptual experiences. Following the idea that physiological components are the expression of internal emotions, researchers have focused their studies on facial expressions as involuntary manifestations of ANS activation of valence (Ekman, 1992; Mauss et al., 2005). For example, the disgust for an odor is reflected in facial expressions with lowered eyebrows, wrinkled nose, and lower lip raised (Ekman & Friesen, 1971; Seubert et al., 2010). These specific movements in facial muscles can be recorded and discriminated with high reliability (Ekman & Friesen, 1978; Sayette et al., 2001). The Facial Action Coding Scheme (FACS) measures changes in facial movement based on the analysis of specific regions in the face. FACS identifies 46 different facial features using a 1–6-point rating scale (Ekman & Friesen, 1978). It was originally developed to catalog the diversity of human facial expressions with broad applications in many fields of study.

The emotional FACS (EMFACS), an adaptation of the original FACS, was specifically designed to make inferences about nonverbal basic emotions. Subject are videotaped, and the images are manually coded by trained assessor or computer analyzed using automated software such as automated facial expression analysis (AFEA). FaceReader^{TM} is a well-known commercial software package that uses this approach. FaceReader^{TM} has been employed to differentiate samples of orange juice based on facial expressions and to characterize emotional reactions to different food odors such as orange and fish. Results showed that disliked samples evoked faster and more robust adverse facial expressions than liked samples (Danner et al., 2014; He, Boesveldt, et al., 2016). One study showed that fish odor, commonly known to be unpleasant, evoked expressions of disgust after just 100 ms, whereas positive expressions induced by orange odor occurred more slowly, after 1700 ms (He et al., 2014). However, more work needs to be done to address the internal validity of these methods.

Facial coding has been used in conjunction with self-reported tools such as PrEmo®, in which subjects self-assess their emotions by pointing and clicking on drawings of positive and negative cartoon animations. When used together under conditions of continuous monitoring, these techniques were capable of distinguishing the time course of arousal from that of valence. In a study investigating two common food aromas in three different concentrations, He, Boesveldt et al. (2016) observed strong and immediate associations (after 2 s) between aroma presentation, facial expressions, and arousal and robust but slower associations with valence after 4 s (He, de Wijk, et al., 2016). In another study, Beyts et al. (2017) showed that some small facial muscle movements differentiated aroma stimuli rated as unpleasant from those that were positive or neutral.

Some regions of the face, such as the eyes, may be more revealing of emotional status than other facial areas. This understanding has fueled the popularity of eye tracking techniques (Lim et al., 2020) to measure emotions using a variety of parameters including pupil diameter and position, blink duration and frequency, direction of motion, speed, and fixating duration of the eye. Using a machine learning technique (Raudonis et al., 2013) showed that eye tracking recognized four predefined emotional categories from eye movements. Lim et al. (2020) recently reviewed the literature on eye tracking technology and concluded that pairing eye tracking with other measures such as EEG recording and facial recognition increased emotion detection (Lim et al., 2020).

The possibility of reading consumer emotions via facial recognition and eye tracking has generated much interest among food and beverage researchers and has spurred the development of a new field loosely described as "neuromarketing" (McClure et al., 2004). Generally speaking, facial expressions are better indicators for disliking more than liking both in children and young adults (de Wijk et al., 2012, 2014; Zeinstra et al., 2009). In addition, facial expression analysis revealed significant correlations between the emotional term "happy" and liking after participants consumed orange juice (Danner et al., 2014), and between sad, disgusted and angry for disliked foods (de Wijk et al., 2012).

Unavoidably, the process of chewing a semi-solid or solid food alters the measurement of facial expressions. For example, Kostyra et al. (2016) attempted to record facial emotions when subjects tasted and swallowed ham samples. However, the rich complexity of facial expressions was lost after swallowing (Kostyra et al., 2016).

5.4 | Summary: Physiological measures

CNS recording such as fMRI and ANS measures including HR, RR, and skin conductance provide reliable representations of our internal state of arousal, but they may be less useful in characterizing valence, the degree to which a stimulus tracks with positive or negative feelings. Measuring multiple parameters in the same study may produce more complete emotional profiles than single measures, but sometimes individual measures do not agree. It is important to recognize that some workers reject the notion that singular emotions are a direct reflection of physiological changes, raising doubts about the value of physiological measurement to predict emotional experiences (Thomson & Coates, 2021). This is a controversial topic in the field and readers are referred to (Barrett et al., 2019) for further discussion of this issue.

The analysis of facial expressions is a popular and useful tool for measuring emotional variations in adults, children, and infants. The power of facial analysis is counterbalanced by many pitfalls and drawbacks. For example, the interpretation of the videotapes is challenging and time consuming. The validity of the results depends on the expertise of coders, who must undergo intensive training. The coding can be automated, but the validity of the results depends on the algorithms used (Cohn & Ekman, 2005). The reliability of measuring emotions from facial expressions has also been questioned. A recent meta-analysis by Barrett et al. (2019) concluded that evidence supporting the ability of an observer to accurately "read" or interpret the facial expression of another individual is weak. An earlier meta-analysis revealed that facial configurations had stronger reliability among individuals within the same culture than between different ones (Elfenbein & Ambady, 2002). This could have implications for interpreting facial expressions from heterogeneous populations which are common in consumer studies.

With all the above considerations in mind, we suggest caution in selecting the physiological methods to use and a conservative approach in interpreting the results. The current lack of consensus in this field underscores the need for more research.

6 | FACTORS THAT INFLUENCE EMOTIONS

Aroma and flavor perception and liking are influenced by a large number of factors including stimulus intensity, age, gender, hunger/satiety status, time of day, previous experience, and cultural background (Ayabe-Kanamura et al., 1998; Delplanque et al., 2008; Doty et al., 1985; Parma et al., 2015; Yeshurun & Sobel, 2010). Understanding why consumers accept or reject a particular product can help food developers fine-tune their products to appeal to a specific consumer segment. As discussed in previous sections, emotional reactions to foods provide an additional measure of product acceptability and satisfaction, beyond liking. Thus, it seems reasonable to ask whether individual differences in emotional reactions to foods are also involved in consumer behavior as recently suggested by Cardello and Jaeger (2021). The following sections address this novel area of food emotions research with a particular emphasis on the role of genetic differences in taste and smell.

6.1 | Personal traits and situational factors

Research on the influence of individual differences on emotional reactions to aromas is limited, but a few of these factors have received at least some attention in the literature. For example, wine consumption evoked higher scores in rating the emotional response in females than in males (Mora et al., 2018), and the elicited emotions were found to be dependent on personality trait (Mora et al., 2019). Several studies have shown that the mode of delivery or the concentration of a stimulus can modify mood intensity and/or valence (Doty et al., 1986, 1995; L. M. Jin et al., 2018). In one study, emotional responses collected using the EsSense Profile® were stronger when obtained online than in a laboratory environment (Jaeger & Hedderley, 2013).

It has also been shown that time of day in combination with the eating environment affects emotional expression, with a higher frequency of positive emotions when foods are presented in an appropriate or expected context (Piqueras-Fiszman & Jaeger, 2014a, 2014b, 2014c, 2015), or with a different emotional profile for beer according to real or virtual recreated contexts (Worch et al., 2020). Indeed, when experimental conditions are kept constant except for the testing location, food consumption at home triggered higher HR and more intense facial expression compared to laboratory consumption (de Wijk et al., 2019).

6.2 | Individual differences and genetic variation in reactions to flavor

As stated previously, consumers express highly personal likes and dislikes for a wide range of foods and beverages that often reflect individual differences in sensitivity to specific aromas, flavors, and tastes (Drewnowski, 1997). For example, large individual differences in perceptual ability have been observed for isovaleric acid found in pungent cheeses, for cis-3-hexen-1-ol, a grassy-green aroma found in certain fresh fruits and vegetables and for diacetyl, a major component of butter aroma (Lawless et al., 1994; Tempere et al., 2011). Individual differences have also been reported for β-ionone, a fruity/floral aroma found in wine and used as a flavoring ingredient in processed foods (Jaeger, McRae, et al., 2013; Peng et al., 2016), and (E)-2-decenal, responsible for grassy-green/soapy flavor of cilantro that many individuals find objectionable (Eriksson et al., 2012).

A growing literature has documented associations between these perceptions and variation in genes involved in olfaction. For example, one study showed that a single-nucleotide polymorphism (SNP) in the olfactory receptor gene *OR6A2* was strongly associated with the soapy-taste of cilantro (Eriksson et al., 2012). Another study reported a relationship between a SNP in the *OR51B5* gene and perception of cinnamon aroma (Concas et al., 2021). Importantly, much of the work on olfactory genes has focused on the perception of pure compounds (Fu et al., 2019). Less is known about genetic differences in the perception of complex flavors that characterize everyday foods.

The findings on β-ionone cited above by Jaeger et al. are particularly compelling in showing how genetic studies linked to emotions can inform our basic understanding of aroma/flavor perceptions and provide insights for optimizing consumer product choice and acceptance. Specifically, subjects with sensitive alleles at a particular locus in olfactory gene, OR5A1 rated low concentrations of β-ionone as peaceful, warm, and happy, while subjects with insensitive alleles did not differ in emotion perception between β-ionone and the neutral odor of pure paraffin. Interestingly, at high concentrations both groups reported negative emotions. Nevertheless, when β-ionone was added to milk chocolate or apple juice, sensitive individuals preferred the unsupplemented versions (Jaeger et al., 2014). These findings underscore the power that genetic differences can potentially exert on consumer responses to products formulated with seemingly common flavor and fragrance materials. To our knowledge, researchers have yet to comprehensively examine the role of other olfactory genes in aroma perception and emotions, for a better understanding of consumer acceptance of products. This area is fertile ground for future research.

Finally, genetic differences have also been reported in binding proteins and other signaling elements that modify perceptions. Specifically, olfactory binding proteins (OBPs) help transport odorants to sensory cells in nasal mucus. A polymorphism in the gene coding for human OBPIIa has been associated with variations in retronasal perception where the major allele is associated with higher sensitivity and expression of the protein relative to the minor allele (Melis et al., 2019; Sollai, Melis, Magri, et al., 2019; Tomassini Barbarossa et al., 2017). The extent to which OBPs may modify the emotional impact of perceptual experiences should be further investigated.

7 | BITTER TASTE, PROP STATUS, AND EMOTIONAL REACTIONS TO FOODS

Humans possess a large repertoire of 25 different bitter receptors collectively known as the TAS2R (bitter) receptor family (Behrens et al., 2009). This large number of receptors may have provided an evolutionary advantage to our preindustrial forebearers to avoid bitter-tasting phytochemicals which might also be toxic. Variation in some *TAS2R* genes has been associated with differences in perception and liking of bitter and strong-tasting foods. Examples include variation in *TAS2R19* associated with grapefruit juice, the complex of *TAS2R -3,-4,-5* and coffee (Hayes et al., 2011) and *TAS219* and quinine (Reed et al., 2010). Although this review focuses on the genetics of bitter taste, genetic variation in genes related to sweet and salty taste has also been examined although relationships may not be consistent (Barragan et al., 2018).

The most closely studied trait in human taste biology (Bartoshuk, 1993) is the genetic variation in perception of the bitter thiourea compound phenylthiocarbamide (PTC) that was first discovered by Fox (1932). Responsiveness to thiourea compounds exemplified by PTC and a related compound, 6-n-propylthiouracil (PROP) ranges from undetectable by some individuals to intensely bitter by others. Based on PTC/PROP-tasting ability, the population can be divided into nontasters who are taste blind to these compounds, medium tasters, who perceive them as moderately bitter and super-tasters who experience extreme bitterness from these compounds (Bartoshuk et al., 1994; Tepper, 2008). A variety of screening methods can be used to classify individuals by their taster status (Tepper et al., 2017).

Approximately 30% of Caucasians in North America and Western Europe, are non-tasters, ~45% are medium tasters, and ~20% are super-tasters (Bartoshuk, 1979; Bartoshuk et al., 1986). However, this distribution varies markedly in different populations around the globe. For example, the percentage of nontasters in some populations in sub-Saharan Africa, East Asia and India, is estimated to be 18%, 11%, and 43%, respectively (Guo & Reed, 2001). This worldwide diversity can make it very challenging to assess the role of this phenotype in food research with ethnically-mixed consumer groups.

The ability to taste PROP is linked to variation in the *TAS2R38* bitter-taste receptor gene (Bufe et al., 2005; Kim et al., 2003). Variation in this gene gives rise to two alleles, PAV, the sensitive form and AVI the insensitive one. Since humans possess two copies of each allele, nontasters carry two copies of the insensitive form (AVI/AVI). Super-tasters carry two copies of the sensitive form (PAV/PAV) and medium tasters possess one copy of each form (PAV/AVI). It is important to note, however, that the correspondence between *TAS2R38* genotype and PROP tasting is not a perfect one as some PAV/AVI carriers may perceive more extreme bitterness from PROP than PAV/PAV carriers and vice versa. This suggests that the PROP-tasting phenotype is malleable and can be modified by many factors including age, gender, ethnicity, tobacco use, and body weight (reviewed in Tepper et al., 2017).

PROP tasters, especially super-tasters, perceive more bitterness from cruciferous and other green vegetables and they often dislike these vegetables more than nontasters (Drewnowski et al., 1999; Turnbull & Matisoo-Smith, 2002). These differences can be attributed to the presence of glucosinolates, the naturally occurring analogs of PROP and PTC in these foods (Prescott & Swain-Campbell, 2000; Tepper & Nurse, 1998; Yeomans et al., 2007). In addition, PROP tasting is associated with greater perception and lower liking of sweetness, fattiness, astringency and oral irritation from alcohol and chili pepper (Prescott & Swain-Campbell, 2000; Tepper & Nurse, 1997). These differences arise from variation in taste anatomy where super-tasters have been shown to have more fungiform taste papillae and more trigeminal nerve fibers (Bajec & Pickering, 2008; Bartoshuk et al., 1994; Melis et al., 2013). Greater papillae density in super-tasters is also associated with variation in the gustin gene (CAV6), which has been implicated in the regulation of taste bud density and functionality. Interested readers can refer to the work of Padiglia et al. (2010), Melis et al. (2013), Barbarossa et al. (2015) for a description of these mechanisms

These diverse features of PROP-tasting (and *TAS2R38* gene variation) are not shared with other TAS2R genes, underscoring its unique role as a general marker for oral sensations with broad implications for food preferences, diet selection, and health. That being said, it is important to acknowledge that not all studies support this conclusion. For example, one study showed no relationship between PROP status and dietary patterns in women and another study showed a positive rather than a negative association between *TAS238* variants and liking of bitter foods in wine consumers (Drewnowski et al., 2007; Fu et al., 2019). This lack of agreement only emphasizes the complex nature of gene effects on human taste perception and food selection.

There is evidence to suggest that general emotional reactivity may be higher in super-tasters than in nontasters. In one study where subjects were asked to rate their emotions before and after watching videos evoking rage and sadness, PROP tasters reacted more intensely than nontasters, especially with respect to anger (Macht & Mueller, 2007). Herbert and coworkers examined whether emotional reactivity (measured with eye blink and pupil response) differed between PROP groups while viewing emotion-evoking pictures. In contrast to nontasters, eye response in super-tasters was significantly different in the viewing of affective compared to neutral pictures, revealing an immediate tendency for avoidance after an emotional stimulus (Herbert et al., 2014). These findings are consistent with earlier work demonstrating that PROP sensitivity is related to higher disgust and emotional arousal (Herz, 2014; Macht & Mueller, 2007).

In a unique study, Robino et al. (2016) examined the role of PROP status in alexithymia, which measures the inability to conceptualize personal emotion states. Results showed that nontasters were less aware of their own internal emotional state evidenced by higher scores on the alexithymia scale. In addition, alexithymia was associated with reported food choices and preference for sweets, fat-containing foods and alcohol (Robino et al., 2016).

A number of studies have assessed the role of PROP status in the acceptance/rejection of chili pepper and spicy foods which are strongly influenced by emotions and attitudes including variety-seeking, sensitivity to punishment, and reward and other traits (Byrnes & Hayes, 2013; Nolden & Hayes, 2017). Among PROP tasters, those who were defined as food adventurous liked chili and hot sauce more than PROP tasters who were classified as nonfood adventurous (Ullrich et al., 2004). Liking of chili was found to be a function of PROP status, with higher scores in non-tasters than in super-tasters when studied in two different Italian populations (Spinelli et al., 2018; Tepper et al., 2009). Collective evidence revealed a strong correlation between certain personality traits (i.e., sensation seeking and risk-taking) and liking and intake of spicy food (Byrnes & Hayes, 2013, 2016). Spinelli et al. (2018) also reported that PROP responsiveness was positively correlated with alexithymia in females, and that females with higher alexithymia scores perceived higher burning intensity. However, other studies reported no correlation with pungency of spicy food and PROP sensitivity (Bajec & Pickering, 2010; Törnwall et al., 2012).

One study examined emotional reactions of consumers classified by PROP status to beers differing in bitterness, carbonation, and serving temperature. In general, the beers evoked more positive emotions (higher "excited" and "content" ratings) and lower "bored" ratings in super-tasters compared to nontasters (Yang et al., 2018).

With the exception of the study by Yang et al. (2018) reviewed above and some limited data from Scott et al. (2019) showing an interaction between PROP status and "disgust" on liking of chipotle-flavored soup, there are no other reports on the influence of PROP status on emotional reactions to foods. To begin to address this gap in knowledge, we conducted a small pilot study examining the emotional responses to six complex food aromas in PROP super-taster and nontaster groups that are viewed as pleasant by most people (e.g., strawberry, coconut, and spearmint) or polarizing (e.g., Brussels sprouts, cilantro, and mustard). Figure 6 shows preliminary data on the selection frequency of the "mostly" mood terms from the Mood Signature Questionnaire (described previously) by PROP nontasters and super-tasters. The mood terms were categorized as "positive" or "negative" and compared between the two groups. Generally speaking, aromas of strawberry, coconut, cilantro, and spearmint evoked positive emotions in most subjects regardless of PROP status. The aroma of Brussels sprouts evoked the opposite response of negative emotions in most subjects. The one exception was mustard aroma, where there was a strong trend for super-tasters to assign negative emotions to this aroma and nontasters to view it as positive. These findings are preliminary but suggest that PROP status may play a role in emotional reactions to some polarizing food aromas.

8 | FUTURE PERSPECTIVE

Over the past few decades, much of the progress in understanding the role of emotions in food acceptance has focused on the development of improved methods. In the realm of self-reports, workers fine-tuned questionnaires for specific products, age groups, geographic areas, and

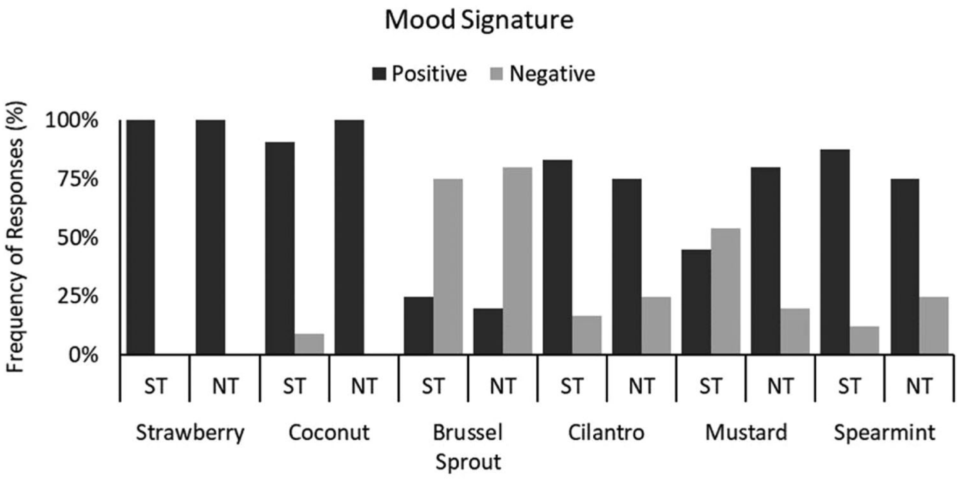

FIGURE 6 Selection frequencies of the mostly mood terms for the Mood Signature Questionnaire (ST, $n = 8$; NT $n = 4$ for strawberry, cilantro, and spearmint; ST, $n = 11$, NT, $n = 5$ for mustard, Brussels sprout, and coconut). Unpublished data

cultural background. Survey methods that were most discriminating but also less fatigue producing were identified. Despite the many limitations of questionnaires, such as cognitive bias, being retrospective in nature, and time consuming, they seem to discriminate emotions better than physiological measures, and they have more relevance for understanding liking responses.

ANS measures such as HR and SCL are valuable for detecting differences in arousal, but they may be less useful for discriminating valence and/or specific emotions. Analysis of facial expressions and fMRI techniques are powerful tools, but they also have shortcomings in identifying the rich complexity of emotions related to taste/smell stimuli. Studies combining physiological measurement and self-reported techniques might ultimately provide a more nuanced understanding of human emotions in response to foods. Undoubtedly, methods will continue to evolve and improve to achieve this goal.

Finally, studies have just begun to scratch the surface of our understanding of individual differences, especially genetic variations and their role in emotional reactions to foods. Including genetic testing (DNA analysis) in typical consumer studies is clearly not feasible. Nevertheless, a great deal can be learned from laboratory-based genetic studies, informing the interpretation of consumer responses. The one exception is PROP screening which does not involve the collection of genetic material and can be easily incorporated into laboratory-based studies, central location, and home-use tests using simple and rapid procedures (Zhao et al., 2003). The consideration of individual differences in food emotions research may lead to important advances in product formulation and marketing, consumer satisfaction, and nutritional health and wellbeing.

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AUTHOR CONTRIBUTIONS

Mariano Mastinu: Conceptualization; Writing – original draft. Melania Melis: Writing – original draft. Neeta Y. Yousaf: Writing – original draft. Iole Tomassini Barbarossa: Funding acquisition; Writing – review & editing. Beverly J. Tepper: Conceptualization; Funding acquisition; Writing – review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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