Influence of Sensation and Liking on Eating and Drinking

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Contents

Abstract

Flavor is an integrated unified perceptual phenomenon that arises from inputs across multiple sensory modalities, including taste, smell, chemical touch (chemesthesis), and oral somatosensation. The flavor of foods influences the decisions we make about what foods to eat, and in an environment with abundant options, this primarily occurs by causing us to reject certain foods because we do not like the sensations they evoke. In general, bitter sensations

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tend to be disliked, while sweet sensations are liked; data on other taste qualities are less clear. Notably, there are substantial differences between people, both in their sensory and affective responses, and learning and exposure can decouple sensations from innate aversive responses. Further, dynamic changes in liking within a meal also influence the amount of food we eat.

Introduction

To the average person on the street, the flavor of a food is typically viewed as an inherent property of the stimulus (i.e., the food). That is, apple flavor comes from an apple, potato chips are salty, and sugar is sweet. A variant of this belief is also shared by many food chemists or product developers with in the food industry: if I wish to formulate a grape-flavored drink, I simply obtain a natural or synthetic flavor (like methyl anthranilate) from a supplier and add it to my product. However, this essentialist view misses a critical point: flavor is a perceptual phenomenon (i.e., a percept), meaning it occurs in the brain, not the bottle. That is, the percepts we experience from foods are not only the result of the integration of multiple physiologically distinct sensory systems but also prior experience and learning. If I have never been exposed to the odorant cis-rose oxide, I will likely struggle to describe it, but if I can, I will probably say it has a generic fruity odor. However, to other individuals, the sensation of cis-rose oxide is very clearly the characteristic flavor of lychee fruit or an Alsatian Gewürztraminer wine. As we chew the lychee, the overall flavor emerges from the volatiles sensed via olfactory receptors, but also the sweetness of the sugars and the sourness and astringency of the organic acids. A review of the biological and physiological processes that underlie these sensations is provided elsewhere in this handbook (see Duffy and Hayes forthcoming). The focus of this chapter is on flavor perception, the relationship of food sensations to liking and eating, and factors that complicate these relationships.

A General Framework Linking Sensation to Eating Behavior, via Affective (Hedonic) Responses

It is widely and broadly accepted that the sensory properties of food have a substantial influence on ingestive behavior: at home, parents add salt to cooked vegetables prior to serving; at the café, patrons add sugar and/or cream to their coffee; and in research and development labs around the globe, food companies spend millions of dollars each year to optimize their formulations. However, it is also fair to state that the sensory properties of food are only one small factor among many that influence behavior regarding the consumption of foods and beverages, as evidenced by numerous other chapters in this handbook. Still, a convincing argument can be made that the sensory properties of foods and beverages influence both food choices and termination of eating within a meal via changes in pleasure. This chapter provides a brief overview of these data.

When we add salt to our food, or sugar to our coffee, we change the amount of saltiness or sweetness in that food, and the lawfulness of these relationships has been studied for decades by psychophysicists, sensory scientists, and food technologists (e.g., Holway and Hurvich 1937; Schutz and Pilgrim 1956; Pangborn 1963). In turn, the observation that the pleasure arising from a sensation varies as a function of intensity or concentration is not new (e.g., Pfaffmann 1960). Indeed, in 1874, Wilhelm Wundt, the founder of experimental psychology, noted that pleasantness increased with sensation intensity, before peaking, and then falling as sensation continues to increase. For taste, this was first shown experimentally in 1928 by Engel for sourness and saltiness (see Pfaffmann 1980). Some have characterized the point of maximal pleasure, that is, the point at which the curve turns over (i.e., the second derivative) as the "bliss point" (Moskowitz 1981). However, in practice, this is probably a misnomer, as extant data indicate this region is more of a plateau in practice, as consumers are actually quite tolerant (i.e., insensitive) to formulation changes near this point (e.g., Li et al. 2014b; Rolon et al. 2017). Other data also indicates there are large and robust individual differences in the shape of the concentration-pleasure curve (e.g., Garneau et al. 2018; Iatridi et al. 2019a, b) that are largely obscured when only mean responses are considered (cf. Lundgren et al. 1978 and Moskowitz 1971). Still, if one assumes that humans are pleasure maximizing, or at least pleasure seeking, then it typically assumed that greater liking drives greater intake. This assumption is generally well supported by evidence in adults (de Graaf et al. 2005; Tuorila et al. 2008; Johnson et al. 2014; Byrnes and Hayes 2016; Park et al. 2018) and children (Caporale et al. 2009; Vosburgh et al. 2019) for both foods (e.g., Dinehart et al. 2006) and beverages (e.g., Lanier et al. 2005).

Collectively, the three pairs of relationships described above – concentration-sensation, sensation-pleasure, and pleasure-intake – result in a causal chain that links the formulation of a food product to consumption. However, the correlations of each step along this chain are far less than one, both due to statistical attenuation due to measurement errors (see Hayes 2015) and other factors that meaningfully modify these individual relationships (e.g., genetic variation, cost, availability, branding, dietary restraint, cultural factors, moral disgust, etc.). By one rough approximation, the total variance in intake that can be explained by formulation is actually quite low, somewhere between 2% and 22% (Hayes 2018). On the other hand, centuries of culinary traditions (including the historical quest for spices that quite literally drove exploration, colonization, and global trade), as well as the continual expenditure of substantial resources for formulation and reformulation over many decades by global food companies, imply the putative framework linking food formulation and sensation to intake via affective responses (see Fig. 1) must have some degree of face and predictive validity.

The following sections provide a discussion of various complications to the framework presented in Fig. 1. For additional information and discussion of this conceptual framework, the interested reader should also see Hayes (2015).

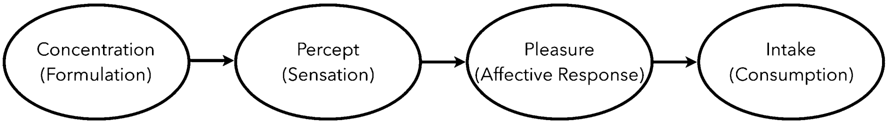

Fig. 1 A working model of how food composition is related to intake via pleasure

The Imperfect Relationship Between Food Liking and Food Selection or Intake

As noted above, most researchers accept that liking is positively (if imperfectly) related with intake. This has been repeatedly found by multiple researchers on multiple continents across multiple decades for multiple types of foods, with correlations in the literature ranging from +0.22 to +0.81 (e.g., Schutz 1957; Cardello and Maller 1982; Zandstra et al. 1999; Tuorila et al. 2008). For example, Lähteenmäki and Tuorila found the correlations between liking and use of chocolate, ice cream, licorice, flavored yogurt, cookies, and soft drinks were between +0.57 and +0.73 in Finish women (Lähteenmäki and Tuorila 1994), while Byrnes and Hayes found that the correlation between liking for the burn of a spicy meal and annualized intake of chili-containing foods was +0.58 in adults in the United States (Byrnes and Hayes 2013). These reports provide strikingly similar estimates to an early report from Schutz (Schutz 1957): he found that the now famous 9-point hedonic scale (Peryam and Pilgrim 1957; Meiselman and Schutz 2003) predicted both the amount taken and amount eaten by American military personnel in an ad libitum setting, with correlations between +0.51 and +0.77. More recent work suggests food liking questionnaires also predict dietary biomarkers (Sharafi et al. 2015) as well as aggregate measures of dietary quality in American adults (Zoghbi et al. 2017) and children (Sharafi et al. 2015) and Australian adults (Wanich et al. 2019).

As these examples illustrate, various studies have operationalized liking and intake in different and diverse ways – various consumption estimates include direct observation of amounts eaten or amounts taken, self-reported intake of specific foods, comprehensive diet records/food diaries, and data drawn from validated food frequency questionnaires, while affective responses are typically estimated from acute tasting of foods or longer surveys of multiple foods using some type of liking or pleasantness scale (i.e., so-called food preference questionnaires). While this heterogeneity complicates direct comparisons, it also provides some degree of convergent validity, which enhances the robustness and generalizability of the findings. Direct head-to-head comparisons of liking of sampled foods and surveyed liking (i.e., names on a list of foods) are far less common, although a few reports suggest this relationship is also positive, in the range of +0.43 to +0.64 (Hayes et al. 2010; Sharafi et al. 2012).

The consistent and robust positive association between various measures of liking and intake leads to the common conclusion that greater liking drives greater intake. At the extremes, this widespread assumption has led some to suggest that decades of optimization of foods by the food industry has somehow made these foods hyperpalatable or even addictive, thereby contributing to the obesity epidemic seen in industrialized nations (Kessler 2009; Moss 2013).

However, a deeper analysis of the liking-intake relationship suggests the common assumption that greater liking leads to greater intake, although extremely widespread, is incorrect, or at least, is insufficiently nuanced. Specifically, the relationship between liking and intake is heteroscedastic – that is, the data tend to have a cone shape when visualized in a scatterplot. As shown in Fig. 2, the variance in intake is quite small when liking is low, whereas the variance is much larger when liking is high. The data in the left and center columns show self-reported liking and intake data for a group of high-fiber foods (whole grains, fruits, and vegetables) and high-fat foods (fried foods, red meat, processed meats, oil and high-fat condiments, whole-milk dairy, cookies, cakes, and pastries) for 88 women from a worksite health promotion program in Connecticut (Duffy et al. 2009), while the rightmost column shows self-reported liking and intake data for chili-containing foods for 97 adults (18–45 years) in a laboratory study in Pennsylvania (Byrnes and Hayes 2013).

Practically speaking, the heteroscedasticity in these plots suggests that rather than being a driver of intake, affective responses act as a ceiling or break on intake – or to put it more simply, instead of the classical conclusion that more liking drives more intake, a better conclusion would be that *disliking drives nonuse*. Personally and intuitively, this should make sense. A person may really love large, well-marbled steaks and bold tannic Chianti wines from Italy, but still moderate their intake of each due to health concerns or cost or myriad other factors (e.g., Herman et al. 2019; Higgs and Ruddock 2019). Indeed, this point can be clearly illustrated in the bottom half of Fig. 2 by comparing the two shaded regions within each panel: when a food is disliked (i.e., is rated below neutral), almost no individuals consume it frequently (top left shaded region), whereas when a food is liked (i.e., is rated above neutral), many individuals still fail to regularly consume those foods (bottom left shaded region). For foods like fruits and vegetables, this discordance may represent cost or availability constraints or preferences of other members of the household. Conversely, for energy-dense foods, discordance between liking and intake may be an indirect measure (proxy) for dietary restraint in adults. Indeed, among American women, those who were discordant in this way (i.e., high liking/low intake) had significantly higher restraint scores on the Three-Factor Eating Questionnaire (Sharafi et al. 2018). In children, this same kind of discordance (i.e., high liking/low intake for high-fat/sweet/salty foods) associates with greater body mass index percentiles relative to the concordant low liking/low intake group, suggesting parents of these children may be restricting intake of foods they view as being unhealthful (Sharafi et al. 2015).

The idea that disliking discourages intake is not limited to self-reported assessments of chronic diet, as some controlled laboratory studies and naturalistic free-living feeding studies show similar effects on food intake and food choices. In one study of intake by US Army personnel under field conditions between 1995 and 1997 (de Graaf et al. 2005), the relationship between liking and intake was curvilinear, as is shown in Fig. 3. Critically, if a food was rated above neutral, greater

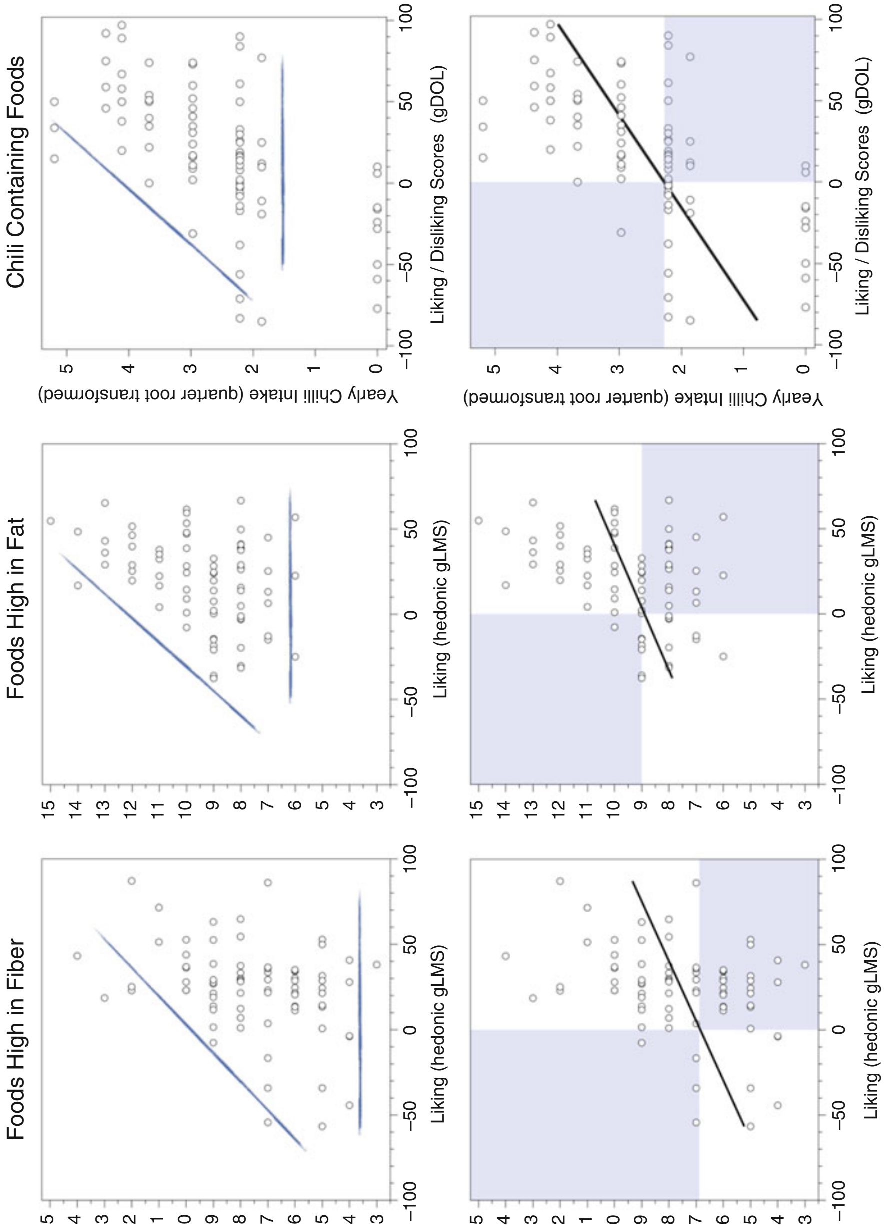

Fig. 2 (continued)

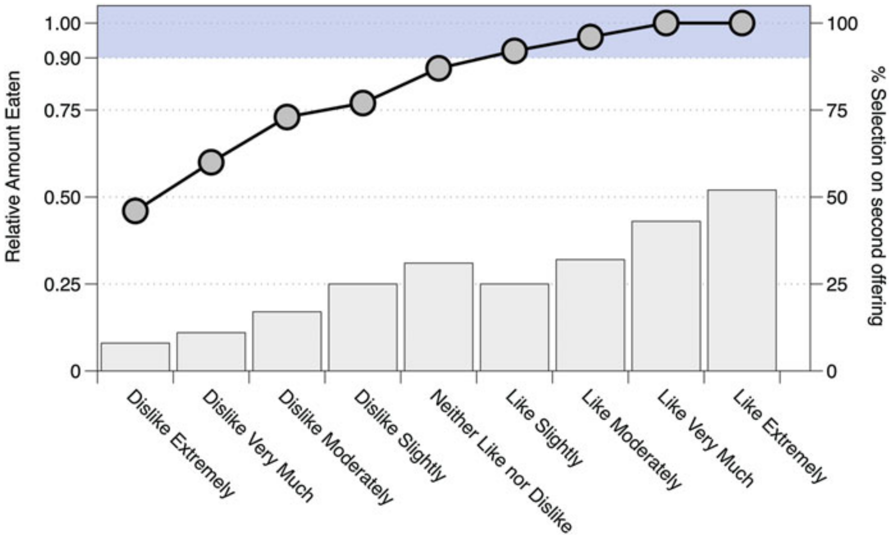

Fig. 3 Relationship between liking ratings and amount eaten on first offering (dots) and percentage of time selected on second offering (bars) under naturalistic feeding conditions with US Army personnel. The shaded region at the top indicates consumption of 90% or more of the food. (Data are replotted from de Graaf et al. (2005). See text for additional discussion)

liking was not a meaningful predictor of greater intake: for the top four categories on a 9-point hedonic scale (like slightly to like extremely), the average amount consumed exceeded 90%. Conversely, soldiers who rated a food as extremely disliked (i.e., a rating of 1 on a 9-point hedonic scale) consumed less than half of it (46%) on the initial offering. These data support the contention that disliking is more closely coupled with nonuse instead of greater liking driving greater intake – that is, disliking acts as a strong barrier to intake. One might argue that this represents a ceiling effect, as hungry troops may have eaten more of highly liked foods had they been available. Indeed, under laboratory conditions, Zandstra and colleagues did find a serving size effect on yogurt intake: under ad libitum conditions, almost all participants (Dutch students) stopped at the initial amount served (300 g), despite being told they could request more if they wished (Zandstra et al. 1999). However, for the soldiers, other data from subsequent offerings suggest that the curvilinear relationship shown in Fig. 4 is not merely an artifact due to serving size or availability. Specifically, when given the opportunity to select the same food a second time (from among several options), foods rated “dislike extremely” were

Fig. 2 Self-reported food intake as a function of liking. (Data are replotted from Duffy et al. (2009) (left and center) and Byrnes and Hayes (2013) (right). The relationship between liking and intake is positive but heteroscedastic, as the variance in intake across the range of liking is uneven. Specifically, the top left corner is empty, meaning people do not eat the food they dislike, whereas in the bottom right corner, some people like those foods but still fail to consume them frequently)

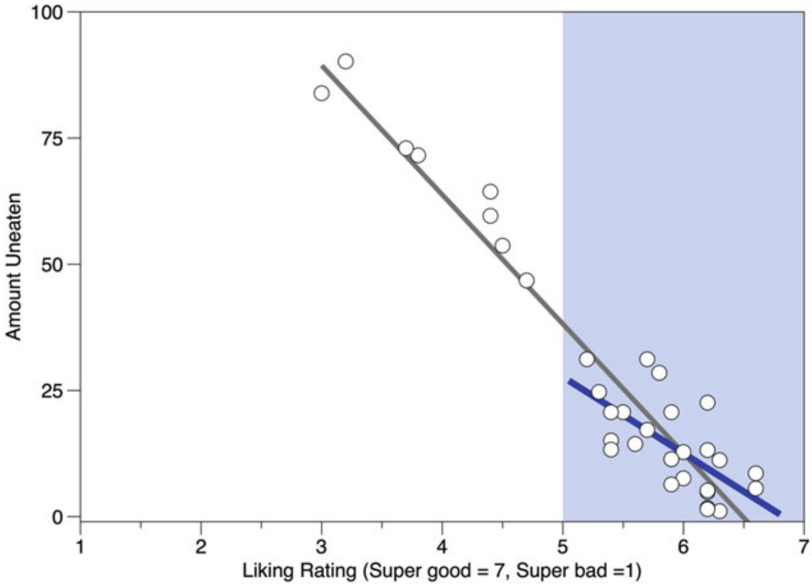

Fig. 4 Relationship between liking ratings and mean amount uneaten for 34 foods by 4- and 5-year-old Italian children under naturalistic feeding conditions (school lunch rooms). The gray line shows the strong negative relationship ($r = -0.96$; $n = 34$) between hedonic ratings and amount uneaten across all 34 foods reported by the authors. The blue line shows that that relationship is weaker, albeit still significant ($r = -0.66$; $n = 26$) when only the well-liked foods are considered (shaded region). (Data are replotted from Caporale et al. 2009)

only chosen 8% of the time, whereas even foods rated as "like extremely" were only chosen 52% of the time (de Graaf et al. 2005). The observation that highly liked foods were only selected about half of the time on a subsequent offering is wholly consistent with the idea that a food being highly liked is not, by itself, sufficient to drive choice or intake.

Nor are such effects limited to soldiers in the field. Mustonen and colleagues asked 62 Finnish women to rank 6 cheeses (full and reduced fat Edam, Emmental, and Havarti) for liking in the laboratory before having them choose three 150 g blocks of cheese to take home; their participants could select 3 of the same cheese, 3 different cheeses, or 2 of 1 and 1 of another. The two cheeses ranked as least liked were only selected ~12% of the time (Mustonen et al. 2007). As a final example, data from 4- to 5-year-old children in Italy also show a strong relationship between disliking and nonuse. Caporale and colleagues asked children to rate their liking of 34 different foods on a 7-point ("super good" to "super bad") scale and then monitored the amounts of these foods uneaten when served in the school lunchroom over the next 2 months (Caporale et al. 2009). Across all 34 foods, they observed a very strong linear relationship ($r = -0.96$) between hedonic ratings and amount uneaten. However, it also appears that the strength of this relationship was driven, in part, by massive underconsumption of the 8 least liked foods: the mean amount left uneaten for the

8 least liked foods was 68%, versus only 14% for the other 26 better liked foods. That is, as shown in Fig. 4, if the eight least liked foods are removed from the analysis, the relationship between liking and intake is weaker, although still significant.

In summary, simple correlations with group means can lead to the common but erroneous conclusion that higher liking leads to more intake, in part due the differential variance intake across the range of hedonic ratings. Instead, the data described here for both self-reports of chronic dietary intake and acute feeding studies under laboratory and naturalistic conditions each seems to suggest a better interpretation would be that disliking drives nonuse for both acute intake and food choices. And this disliking can often be related back to the sensations from the food.

Bitterness: A Signal for Pharmacological Activity and/or Toxicity

Chemicals humans describe as bitter are innately aversive, and stereotypical aversive responses are conserved across species (Ganchrow et al. 1983; Steiner et al. 2001); presumably, these innate responses help prevent ingestion of toxins (Scott and Mark 1987; Katz and Sadacca 2011). Indeed, numerous reports suggest bitterness leads to rejection and/or decreased intake in humans (e.g., Keller et al. 2002; Lanier et al. 2005; Dinehart et al. 2006; Duffy et al. 2010; Harwood et al. 2012a,b). The idea that bitterness is a gatekeeper that guards against toxin ingestion is not new. In 1975, Garcia and Hankins noted bitter stimuli are rejected in humans, and similar rejections are found in monkeys, birds, fish, invertebrates, and protozoa, causing them to conclude rejection of bitterness is a phylogenetically ancient response (Garcia and Hankins 1975).

However, other data challenge the common and persistent view that bitterness is a simple signal to reject a food entirely. In 1994, Glendinning noted many bitter stimuli are not actually toxic (Glendinning 1994), an idea that was recently revisited by Niv and colleagues. Using toxicity data and chemoinformatic tools (i.e., BitterDB (Wiener et al. 2012) and BitterPredict (Dagan-Wiener et al. 2017)), Niv and her team found only 60% of bitterants in BitterDB are toxic and that only 56% of toxic compounds are expected to be bitter (Nissim et al. 2017). This suggests classic assumptions about bitterness and toxicity may be an oversimplification. That is, instead of being a STOP sign per se, bitterness may instead be a CAUTION GO SLOW sign to allow us the opportunity to learn about the stimulus via controlled exposure. The potential medicinal properties of bitter stimuli have been noted for many decades (see Goodman's Pharmacopeia (Goodman and Gilman 1941)), and many beneficial phytonutrients are bitter (Drewnowski and Gomez-Carneros 2000). Likewise, folk medicines like woolly foxglove (digoxin) and cinchona bark (quinine) have a long history of use. Phlorizin, a phenol glycoside isolated from apple tree bark in 1835, was first used as an antimalarial due to its similarity in taste with known antimalarials (Ehrenkranz et al. 2005). The ability of bitterness to act as a marker of potentially desirable pharmacology (versus toxicity to be avoided) is even observed in nonhuman primates (Huffman et al. 2013) and other animals (Villalba et al. 2014). Such therapeutic self-medication by animals (i.e., zoopharmacognosy) presumably requires a mechanism by which the animal can learn to associate specific secondary plant compounds with the beneficial effects of their ingestion.

Similar learning can be commonly observed in humans, as should be apparent from the widespread consumption of black coffee and heavily hopped craft beers. That is, for coffee, the bitterness is aversive initially. But with repeated intake, positive response to caffeine decouples negative affective responses to the bitterness. That is, bitter coffee stops being aversive and may become desirable due to the pharmacological action of caffeine (e.g., Cines and Rozin 1982; Chambers et al. 2007). This process has been termed flavor-consequence learning (Yeomans et al. 2005). In summary, bitterness is innately disliked, and this appears to be evolutionarily important as it is found in multiple species; however, bitterness is not a simple break on intake, as innate aversions to bitter sensations can also be overcome via learning processes, including those involving reward.

Biological Differences in Bitterness Perception What Potentially Influence Food Liking and Consumption

In addition to experiential factors mentioned above, the influence of bitterness on food choice and eating behavior also varies across people due to normal biological variation. The systematic study of individual differences in chemosensation dates back almost a century (e.g., Blakeslee and Fox 1932), with the initial studies on diet and food liking coming later (Fischer et al. 1961; Glanville and Kaplan 1965). Multiple comprehensive reviews already exist elsewhere (Duffy 2007; Hayes et al. 2013; Keller and Adise 2016; Running and Hayes 2016; Ulla et al. 2016; Hayes 2018), so they will not be discussed here in great detail. As one example, the functional consequences of polymorphisms in the *TAS2R31* gene will be presented briefly here. Humans generally find sweetness appealing and desirable, but at the same time, consumers often do not want the calories that accompany bulk sweeteners like sugar, resulting in large commercial demand for various nonnutritive sweeteners (Sylvetsky and Rother 2016; Wee et al. 2018). The sulfonyl amide sweeteners saccharin and acesulfame potassium (Ace K) are widely used in tabletop sweeteners and diet beverages. However, these sweeteners also have a bitter side taste that is experienced by some individuals but not others (Schiffman et al. 1979; Horne et al. 2002); as would be expected, greater bitterness leads to lower liking ratings (Kamerud and Delwiche 2007). These phenotypic differences in sensation are caused by a single amino acid substitution (Arg35Trp) in the *TAS2R31* gene (Roudnitzky et al. 2011). Consequently, genetic variation in the *TAS2R31* associates with differences in suprathreshold bitterness intensity (Allen et al. 2013a,b) and differential liking of Ace K across individuals (Bobowski et al. 2016). The same gene variants also associate with substantial differences in the bitterness intensity of quinine, as well as the liking for grapefruit (Hayes et al. 2015). However, published data associating these variants with food intake is still lacking.

Notably, this specific genotypic variant and the resulting phenotypic differences are only one example of many. The *TAS2R31* variants are independent of variants in *TAS2R4* that are associated with stevia-derived sweeteners (Allen et al. 2013a; Risso et al. 2014) or *TAS2R38* variants that associate with liking and intake of vegetables (e.g., Duffy et al. 2010; Sandell et al. 2014) or alcohol (e.g., Hayes et al. 2011; Beckett et al. 2017; Hayes and Nolden 2017). Nor are such differences restricted to taste, as functional variants have been reported for starch breakdown (Perry et al. 2007; Mandel et al. 2010) and numerous odorants (Keller et al. 2007; Lunde et al. 2012; Jaeger et al. 2013; Mainland et al. 2014). This remains a highly active area of research (e.g., Trimmer et al. 2019), so it seems likely new relationships between genetic variation and eating behavior will continue to emerge.

Sweetness Is Widely Liked, but Optimums Differ Across People

Like bitterness, humans and other mammals show an innate response to sweetness, but unlike bitterness, this response is positive and presumably appetitive. When newborns only a few hours or day old are given sucrose solutions, they exhibit stereotypical facial responses that are interpreted as being positive (Steiner 1977; Steiner et al. 2001). Likewise, when given plain water or carbohydrate sweetener (i.e., glucose, fructose, lactose, or sucrose) solutions, healthy infants 1–3.5 days old drink more of the sweetened solutions than water, and the different intake increased as sweetener concentration increased (Desor et al. 1973), which has been interpreted to mean the newborns like the sweeter solutions more. Similarly, both healthy term and preterm infants increase their sucking rate and sucking intensity when sucrose is provided without any fluid intake (Maone et al. 1990). Other evidence indicates innate appetitive responses to sweetness even predate birth – if amniotic fluid surrounding a fetus is sweetened by injecting the nonnutritive sweetener saccharin into the amniotic sac, the fetus will increase their swallowing rate (De Snoo 1937).

As noted previously, affective responses to increasing concentration of a sweetener generally exhibit an inverted U shape. Notably, children tend to prefer higher concentrations of sucrose as compared to adults (Mennella et al. 2011; Garneau et al. 2018), and this appears to be a true affective shift rather than a mere cohort effect, as the same individuals show a decline in preferred concentration as they age (Desor and Beauchamp 1987). Within parent-child dyads, children also show greater liking for sweet foods (Vosburgh et al. 2019). There is some evidence to suggest increased liking for higher concentrations of sucrose is related to growth associated biomarkers (Coldwell et al. 2009), although other studies fail to confirm this effect (Mennella et al. 2014).

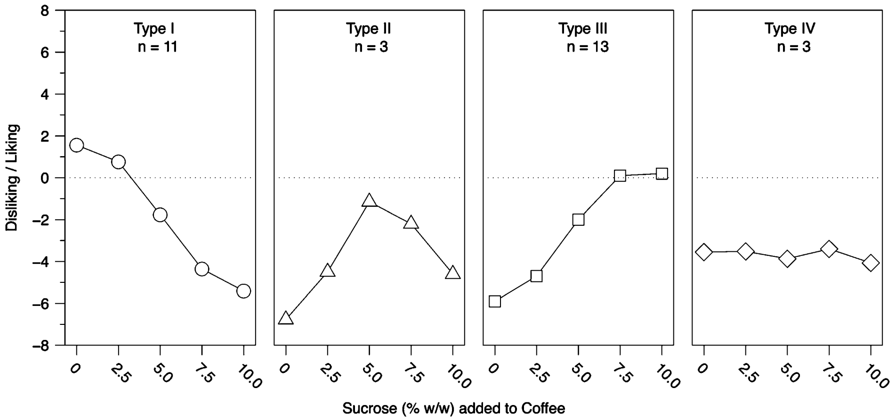

Fig. 5 Illustration of stereotypical patterns of hedonic responses: liking changes as increasing amounts of sucrose are added to instant coffee. (Data are adapted from Lundgren et al. (1978). See text for additional discussion)

While sweetness is innately liked, there are also a large body of work on individual differences in affective responses to sweetness (reviewed by Iatridi et al. 2019b) that dates back many decades (e.g., Pangborn 1970). Irrespective of the differences in sensation summarized in the previous section, individuals also show variation in their affective responses to stimuli. For sweetness, these types of studies have typically segmented people into two to four groups. One early example of this type of work is shown in Fig. 5 – for 30 participants in California in the 1970s, liking generally changes as increasing amounts of sucrose are added to instant coffee, but the patterns of responses also vary widely across groups (Lundgren et al. 1978). Specifically, Type I responders show a monotonic decrease in liking as more sugar is added, while Type II responders show an inverted U pattern. Type III responders show a monotonic increase, and Type IV responders appear indifferent to changes in sucrose, but also dislike all of the coffees. Critically, these data directly challenge the common belief that sweetness is universally liked. Indeed, the authors warn that individual variation needs to be accounted for in reporting sensory data, cautioning that "group averages may be misleading or even completely artifactual (Lundgren et al. 1978)." Regarding sweetness specifically, a recent review identified 71 different papers that segment individuals on the basis of hedonic responses using four major types of methods (Iatridi et al. 2019b). Contemporary methods have shifted toward using hierarchical cluster analysis rather than arbitrary groupings and typically identify three groups rather than four (Kim et al. 2014; Garneau et al. 2018; Iatridi et al. 2019a). The specific biological basis for differences in sweetness preferences has not been determined, but twin studies suggest it has a heritable component (Keskitalo et al. 2007). Several reports indicate that the phenotypic preference groups also differ in liking and intake of sweet foods (Kim et al. 2014; Garneau et al. 2018), and these differences cannot be attributed to simple differences in perceived intensity (Garneau et al. 2018).

Saltiness and Sodium

Using facial reactivity data from infants, multiple studies have found that human newborns do not provide clear affective responses to sodium chloride solutions (e.g., Rosenstein and Oster 1988; Zhang and Li 2006). When combined with older data that fail to show differences in intake for salt solutions versus water for newborns 1–3.5 days old (Desor et al. 1975), these observations are classically interpreted as indicating that responses to salty stimuli are not innate, in sharp contrast to the clear responses seen for bitter and sweet stimuli. Instead, it is assumed that preferences for salt depend on development, maturation, and/or learning, with a critical change occurring around 4 months of age. Specifically, when relative intake of salt solutions and water is compared for infants aged 2.5–6.7 months, it appears preferences for salt develops around 4 months of age (Beauchamp and Cowart 1985), a finding that has been replicated elsewhere (Schwartz et al. 2009). When exclusively breast-fed infants 4–6 months old are given salted and unsalted cereal, they eat more salted cereal (Harris et al. 1990). Similarly, when offered salted carrots versus plain carrots, 2-year-old children put more salted carrots into their mouths, and notably, preferences for saltiness appear to generalize, as the children who ate more salted carrots also consumed more salted foods, as intake of salted carrots was strongly correlated with greater intake of salted soup (Beauchamp and Moran 1984).

However, other data challenge the view that 2- to 4-day-old infants are indifferent to dilute salt solutions: when measures of sucking microstructure (i.e., mean sucks per burst) are compared for salt solutions and plain water, salt is less preferred, on average (Zinner et al. 2002). However, as noted previously, group means can be misleading, as a substantial number of the newborns appeared to prefer the salt solution to water, and strikingly, these preferences were related to both neonatal blood pressure and familial history of hypertension (Zinner et al. 2002). Indeed, newer data for infants tested at 2 and 6 months supports the existence of large individual differences in salt preferences, even prior to the critical 4-month window that is routinely cited (Stein et al. 2006). Looking more broadly across the lifespan, a preference for greater saltiness, like sweetness, appears to be elevated in children, who prefer higher salt concentrations than adults (Beauchamp and Cowart 1990); these shifted preferences may peak in the teenage years (Leshem 2009). In adults, adding salt to real foods like chicken soup or hash browns can increase liking (e.g., Hayes et al. 2010; Lucas et al. 2011), although as would be expected from Wundt, Engel, and Pfaffmann, there can be too much of a good thing, as liking drops when salt level exceeds some optimum (e.g., Hayes 2010; Drewnowski and Moskowitz 1985). There may also be sex differences in optimal levels of salt concentration, although data conflict as to whether men or women prefer higher levels of salt (cf. Hayes et al. 2010 and Leshem 2009).

When discussing salt and saltiness, it is also important to distinguish between the robust sodium appetite seen in some animals and the absence of similar behaviors in humans. Specifically, humans appear to consume salt for pleasure and not to meet a physiological need for sodium. That is, we fail to show clear sodium hunger: unlike many animals (including nonhuman primates), we do not increase our intake of salt when we are sodium deficient. In the words of Leshem (2009), “we will seek salt to please our palate, but not to save our life.”

Sourness

Sourness is generally thought to be a negative taste quality (e.g., Desor et al. 1975; Rosenstein and Oster 1988; Steiner et al. 2001). As a consequence, it has received less attention than other taste qualities as a potential determinant of food preferences. However, sourness is seldom experienced in isolation, and sugar-acid balance is a major determinant of preference for a wide range of foods and beverages. For example, when liking of seedless table grapes by adults is modeled as a function of titratable acidity (which correlates with perceived sourness) and percent brix (i.e., sugar content, which correlates with perceived sweetness), liking rises with increasing sugar content and falls with increasing acid content (Jayasena and Cameron 2008). However, the ratio of brix to acid (i.e., sweetness to sourness) is a substantially better predictor of liking scores than either measure in isolation (Jayasena and Cameron 2008). Similar patterns have also been reported for chokecherry juice (Duffy et al. 2016).

Indeed, the global popularity of Margaritas, Caipirinhas, and lemonade suggests that sourness is not entirely negative, at least when paired with some sweetness. Liem and Mennella (2003) examined perception of and preferences for sour lemon-flavored gelatins in 5- to 9-year-old American children and their mothers. They found that 35% of the children selected the gelatin with highest citric acid concentration (i.e., the most sour sample) as being preferred, and this was not due to inability to sense the sourness, as almost all of the children were able to rank them from most to least sour. This aligns with data from 18-month-old Irish infants, where 23% readily accepted a blackcurrant-flavored drink (Ribena) with the highest levels of added citric acid; notably, fruit intake was greater in the sour-tolerant infants (Blossfeld et al. 2007). Similarly, in 8- to 11-year-old Dutch boys (but not girls), Liem and colleagues found that the preferred sour to sweet ratio for an orange-flavored drink was predictive of reported fruit intake (Liem et al. 2006). In one of the few studies on sourness preferences in adults, participants rated increasing concentrations of citric acid in water as less liked, regardless of age (Chauhan and Hawrysh 1988). Conversely, when presented within the context of an apple-flavored drink, liking first increased to an optimum and then fell as citric acid concentration increased (Chauhan and Hawrysh 1988).

Liking for Odors, Aromas, and Flavors

In direct contrast to the innate responses summarized above for prototypical taste qualities, affective (hedonic) responses to odors and aromas are almost exclusively learned, so no attempt will be made to systematically summarize them here. For more information, the interested reader should see numerous other works on this topic (e.g., Rozin and Vollmecke 1986; Rozin 1990; Birch 1999; Mennella et al. 2001; Sclafani 2004; Mennella and Beauchamp 2005; Yeomans et al. 2008; Prescott 2012; Yeomans 2012; Birch and Doub 2014; Nicklaus 2016). However, it should be noted that these effects are not entirely idiosyncratic and unpredictable across individuals, as shared environments from shared cultural contexts may also provide some degree of generalizability within groups from a specific region (e.g., Pangborn et al. 1988). For example, the affective responses to the presence of the odorant methyl anthranilate in wine appears to vary with geography (Perry et al. 2019). Also, the genetic variability mentioned previously can also interact with learning that may be culturally dependent. The ability to smell the odorants androstadienone and androstenone varies with two amino acid substitutions in the *OR7D4* olfactory receptor gene (Keller et al. 2007). Based on learned associations, some individuals describe these compounds as smelling like urine or body odor. Thus, it is quite understandable that normal variation in this gene can predict differential liking for cooked pork containing these odorants (Lunde et al. 2012).

Taste-Taste Interactions and Cross-Modal Effects

People generally eat foods, rather than tastants in water or simple model systems, and foods are perceptually complex stimuli. Even within very simple model systems with two components, perceptual interactions between sensations can substantially complicate attempts to predict liking (e.g., Lawless 1977). A detailed review of these interactions is beyond the scope of this chapter (and are available elsewhere; see Keast and Breslin 2003; Delwiche 2004). However, two key phenomena – mixture suppression and cross-modal enhancement – will be briefly discussed here.

When two qualitatively different stimuli like bitterness and sweetness are mixed, the perceptual intensity of each is lower in the mixture than the intensity that would be expected had they been presented separately. This is known as mixture suppression. One early example of this comes from Kamen, Pilgrim, Gutman, and Kroll: they found that sweetness from sucrose reduced the bitterness from caffeine, and a smaller suppressive effect was seen for the bitterness of caffeine on sucrose sweetness (Kamen et al. 1961). Subsequent work not only confirmed this effect but also showed that it was due to events in the central nervous system (Lawless 1979; Kroeze and Bartoshuk 1985) rather than being due to some chemical interaction in the mouth or some type of physiological interaction at the periphery. Notably, this effect is asymmetric, as sweetness suppresses bitterness more than bitterness suppresses sweetness (Lawless 1977; Green et al. 2010). Such effects are not limited to model systems, as they also occur in real foods (e.g., Hayes et al. 2011; Li et al. 2014a; Bakke et al. 2018). For example, sweetness suppresses sourness at moderate and high concentrations (Keast et al. 2003), so it should not be surprising that adding sucrose to overly sour chokeberry (*Aronia*) juice improves liking ratings (Duffy et al. 2016).

Taste-taste interactions are also extremely common, both in model systems and real foods (e.g., Frank and Byram 1988; Prescott 1999; Prescott et al. 2004). For example, in general, adding vanilla or vanillin tends to increase perceived sweetness (Lavin and Lawless 1998) regardless of whether participants are asked to use an analytic or synthetic strategy to assess products (cf. Wang et al. 2018, 2019), although these effects are not always observed for all stimuli (e.g., Labbe et al. 2006a; Green et al. 2012). Other odorants also appear to enhance sweetness (Frank et al. 1989; Stevenson et al. 1999; Labbe et al. 2006b; Bartoshuk and Klee 2013). Taste-taste interactions have also been explored as a possible means to facilitate sodium reduction (Lawrence et al. 2009; Nasri et al. 2011). This remains an active area of work, so additional progress is anticipated in the coming decade.

Food Liking Is a Dynamic and Transient Phenomenon

The previous sections have generally assumed that liking for a specific food is a static, stable phenomenon. However, this assumption is not always valid. In 1971, the physiologist Michel Cabanac reported that when a fasted participant was given a sucrose solution and asked to rate the pleasantness, pleasantness ratings dropped when the sucrose solution was swallowed, whereas pleasantness ratings did not change when the sucrose was tasted and expectorated and not swallowed (Cabanac 1971). Indeed, reports of this phenomenon are much much older – for example, the Christian bible notes: “He who is sated loathes honey, but to one who is hungry everything bitter is sweet (Proverbs 27:7).” Cabanac argued this type of shift was part of a regulatory mechanism related to the need state of the body. However, subsequent work by Rolls and colleagues demonstrated that the drop in liking that occurs with repeated exposure to a food within a single meal is due to the sensory properties of the food (Rolls et al. 1981) and not nutritional or metabolic signaling. This effect was thus termed sensory-specific satiety, although more precisely, it should be thought of sensory-specific satiation. (Satiation occurs during a meal and leads to termination of eating, whereas satiety refers to length of time before hunger returns.) This effect should be familiar to anyone who has survived an American Thanksgiving holiday (or any other large feast). After consuming a large amount of salty savory foods, any desire to eat is gone. However, if a sweet dessert like apple or pumpkin pie is offered, the desire to eat a sweet food is not depressed. In a laboratory setting, this is operationalized via a precise experimental paradigm. Moderately hungry participants are first asked to rate the pleasantness of small samples of a battery of foods that vary in their sensory profiles (e.g., sweet, savory, salty, etc.). They are then fed the test meal until the desire to continue eating is gone. Pleasantness ratings are then obtained again for all the foods in the initial battery. Thus, sensory-specific satiety is defined as the relative drop in liking for that specific food (Rolls et al. 1981), not the mere abatement of hunger.

Critically, careful experimentation using this paradigm indicates that these effects are specific to the sensory properties of the food, rather than metabolic signals as Cabanac had hypothesized. For example, pudding and gelatin (jello) sweetened with aspartame (a low-calorie sweetener) or sucrose each cause sensory-specific satiety (Rolls et al. 1988). Nor is this phenomenon restricted to prototypical tastes, as it also occurs for colors and even food shapes (Rolls et al. 1982). That it occurs for something like the shape of pasta is a strong indicator that the effect is cognitive and not physiological in nature and is presumably unrelated to the need state of the body. Separately, repeated exposure over multiple days can also alter liking ratings, as monotonous diets are known to depress intake (Hetherington et al. 2000; Meiselman et al. 2000; Zandstra et al. 2000).

Collectively, these data show that liking is not an immutable property of a food, even for a specific individual, but rather that liking of a food is a dynamic property that varies as a function of context and consumption frequency.

Overall Conclusions

Numerous studies over many decades suggest that greater food intake is positively correlated with greater food liking. However, this is misleading, as merely liking a food does not mean we will choose to eat it, even if we like it very very much. Rather, in an environment where diverse ample food options are available, it is more precise to say that we avoid what we dislike. This disliking is due, in part, to the sensations from food, and these sensations can differ across people.

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