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THE SCIENCE OF TASTE

OLE G. MOURITSEN (red.)

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The Royal Danish Academy of Sciences and Letters
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Copenhagen • Denmark

An Interdisciplinary Symposium • August 11-12, 2014

The Science of Taste

Invited speakers: Gary K. Beauchamp (USA), **Russell Keast** (Australia), **Kumiko Ninomiya** (Japan), **Motonaka Kuroda** (Japan), **Gordon Shepherd** (USA), **Morten Kringelbach** (UK), **Charles Spence** (UK), **Ana San Gabriel** (Japan), **Koji Shimomura** (Japan), **Hiroya Kawasaki** (Japan), **John Prescott** (Australia), **Susanne Højlund Pedersen** (Denmark), **Wolfgang Ahrens** (Germany), **Per Møller** (Denmark), **Takashi Sasano** (Japan), **Michael Bom Frøst** (Denmark)

Organizer: Ole G. Mouritsen, Royal Danish Academy of Sciences and Letters

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Flavour

EDITORIAL Open Access

The science of taste

Ole G Mouritsen

Abstract

An understanding and description of our sensory perception of food requires input from many different scientific disciplines: in addition to the natural and life sciences, human sciences, social sciences, as well as the arts each contributes their perspective on what we call *taste*. For the natural sciences, the key concept is *flavor* encompassing all physical, chemical, and neurophysiological aspects. For researchers in human sciences, psychology, anthropology, and social sciences, *taste* is a broader concept related to tradition, geography, culture, as well as social relations. For cooks and practitioners, taste is a multimodal facet of food and the way we perceive and enjoy it. An interdisciplinary symposium on *The Science of Taste* brought together in August 2014 researchers and practitioners who deal with taste from many different perspectives with an aim to provide a composite mosaic of our current understanding of taste.

Keywords: Taste, Flavor, Research, Science, Cooking

In contrast to smell and the olfactory system, for which the 2004 Nobel Prize in Physiology and Medicine was awarded to Richard Axel and Linda Buck for their discovery of odorant receptors and the organization of the olfactory system [1], our knowledge of the physiological basis for the taste system is considerably less developed [2]. Some progress has been obtained over the last decade by the finding of receptors or receptor candidates for all five basic tastes, bitter, sweet, umami, sour, and salty. The receptors for bitter, sweet, and umami appear to belong to the same superfamily of G-protein-coupled receptors, whereas the receptor for salty is an ion channel. The receptor function for sour is the least understood but may involve some kind of proton sensing.

Notwithstanding the prominent status of physiology of taste and its molecular underpinnings, the multisensory processing and integration of taste with other sensory inputs (sight, smell, sound, mouthfeel, etc.) in the brain and neural system have also received an increasing attention, and an understanding is emerging of how taste relates to learning, perception, emotion, and memory [3]. Similarly, the psychology of taste and how taste dictates food choice, acceptance, and hedonic behavior are in the process of being uncovered [4]. Development of taste preferences in children and gustatory impairment in sick and elderly are now studied extensively to understand the nature of taste and the use of this insight to improve the quality of life.

Finally, a new direction has manifested itself in recent years where scientists and creative chefs apply scientific methods to gastronomy in order to explore taste in traditional and novel dishes and use physical sciences to characterize foodstuff, cooking, and flavor [5-8].

Noting that in general our understanding of taste is inferior to our knowledge of the other human senses, an interdisciplinary symposium, *The Science of Taste*, took place in August 2014 and brought together an international group of scientists and practitioners from a range of different disciplines (biophysics, physiology, sensory sciences, neuroscience, nutrition, psychology, epidemiology, food science, gastronomy, gastroscience, and anthropology) to discuss progress in the science of taste. As a special feature, the symposium organized two tasting events arranged by leading chefs, demonstrating the interaction between creative chefs and scientists.

The symposium led to the following special collection of papers accounting for our current knowledge about the science of taste. The collection includes a selection of opinion articles, short reports, and reviews, in addition to three research papers.

The papers deal with the following topics: the comparative biology of taste [9]; fat as a basic taste [10]; *umami*

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taste in relation to gastronomy [11]; the mechanism of *kokumi* taste [12]; geography as a starting point for deliciousness [13], temporal design of taste and flavor [14]; the pleasure principle of flavors [15]; taste as a cultural activity [16]; taste preferences in primary school children [17]; taste and appetite [18]; *umami* taste in relation to health [19]; taste receptors in the gastrointestinal tract [20]; neuroenology and the taste of wine [21]; the brain mechanisms behind pleasure [22]; the importance of sound for taste [23]; as well the effect of *kokumi* substances on the flavor of particular food items [24,25].

Competing interests

The author declares that he has no competing interests.

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OPINION Open Access

Comparative biology of taste: Insights into mechanism and function

Gary K Beauchamp* and Peihua Jiang

Abstract

Each animal lives in its own sensory world that is coordinated with its diet. In this brief review, we describe several examples of this coordination from studies of the sense of taste, particularly from species of the order Carnivora. This order includes species that are obligate carnivores (e.g., *Felis* species), omnivores, and strict plant eaters. Many of the obligate carnivores have lost function for sweet taste, presumably through relaxation of selection for eating sugars from plants. In contrast, the giant panda, which feeds almost exclusively on bamboo, retains sweet taste function but may have lost amino acid (umami) taste perception. Finally, mammals that have "returned" to the sea, such as sea lions, have experienced even more extensive taste loss, presumably as a consequence of adaptations to a diet of fish and other sea creatures swallowed whole. Future comparative studies will surely reveal important relationships between diet and molecular, cellular, and behavioral taste adaptations that will shed light on how evolution moulds sensory structure and function.

Keywords: Taste, Taste receptors, Comparative studies, Carnivora, Cats, Giant panda, Sea lion, Evolution

Each animal species lives in a separate sensory world that is coordinated with its behavioral ecology. A dramatic example of this occurs for the sense of taste [1] where sensory perception and diet choice are intimately intertwined.

The evolutionary basis for the existence of a small number of primary taste qualities (sweet, bitter, sour, salty, umami, and perhaps a few others) is that these qualities evolved to detect and motivate consumption of critical nutrients and detect and avoid potential poisons. It is widely believed that sweet taste evolved in animals that eat plants to detect energy-rich simple sugars such as glucose, fructose, and sucrose. In contrast, bitter taste presumably functions to insure that an animal avoids poisons; most poisons are bitter and most bitter substances are harmful although this relationship is not perfect. Salty taste is thought to enable detection of sodium, an absolutely essential mineral. When some species of animals become deficient in sodium—usually this occurs in herbivorous animals—a powerful appetite for salty taste is aroused. And for many species, salt is consumed even when there is no apparent need. For sour taste, many have suggested that it is involved in the detection of the ripeness of fruits. Finally, the fifth basic taste, umami or savory, probably serves to signal amino acids and protein. This however remains speculative. Other classes of compounds may also interact with the taste system (e.g., fatty acids, calcium, starch), but they do not give rise to the (to humans) strong qualitative percept that the other five do.

To obtain a clearer understanding of the functional significance for these basic taste qualities, we have studied the order Carnivora. Our goal is to understand how taste receptors and taste perception in different species are related to different feeding ecologies with a particular focus on sweet compounds. For example, some Carnivora species are obligate carnivores (e.g., cats), whereas others are almost completely herbivorous, sometimes feeding on virtually a single plant (e.g., giant panda). If the function of sweet taste is to detect simple sugars in plants, we predict that animals that do not consume plants would not need/have sweet taste perception. By examining sweet taste perception across a number of species in this order, we can put this prediction to the test.

Many years ago, we [2] demonstrated that domestic and wild cats (*Felis* and *Panthera* species) are indifferent to all sweeteners tested but are highly responsive to

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certain amino acids and fats. We speculated that these species may not have the ability to perceive sweet (to humans) sugars. Following the discovery of the major sweet taste receptor, the T1R2 + T1R3 heterodimer (review: [3]), we demonstrated that the cat's indifference to sweeteners can be explained by the pseudogenization of the *Tas1r2* gene which encodes the T1R2 receptor. That is, the sweet taste receptor of the domestic cat as well as closely related wild cats such as lions and tigers has accumulated numerous germ-line mutations of the *Tas1r2* gene, thereby rendering the sweet receptor non-functional [4].

We next reasoned that other exclusively meat-eating species might also have an inactive form of this gene. Sequencing of the entire coding region of the *Tas1r2* gene from 12 Carnivora species revealed that seven of these species, all exclusive meat eaters, had independently fixed a defective *Tas1r2* allele [5]. Since these disabling mutations occurred at different places within the *Tas1r2* gene in each species, this loss of sweet taste function in multiple species in the Carnivora has occurred independently and thus repeatedly during their evolution. Behavioral tests of two of the genotyped species, the Asian otter (defective *Tas1r2*) and the spectacled bear (intact *Tas1r2*), were consistent with the genetic findings: The former showed no preference for sweet-tasting compounds, while the latter preferred sugars and some non-caloric sweeteners. These results indicate that the independent loss of a functional *Tas1r2* is widespread among obligate carnivores. We suggest that this loss is a consequence of the relaxation of selective pressures maintaining receptor integrity.

A striking study with birds provides additional support for the hypothesis that sweet taste exists to detect simple sugars. All birds apparently lack a homolog for the *Tas1r2* gene; this loss likely occurred as the non-avian reptile and bird lines split. Thus, it would seem that birds should not be able to taste sweet sugars. But if this were the case, how can one explain the behavior of avian species that consume sweet sugars such as hummingbirds? Baldwin et al. [6,7] provide one answer: The receptor dimer T1R1 + T1R3, the amino acid or umami receptor in mammals, has been repurposed in these bird species to detect simple sugars thereby opening a novel source of energy not available to many other birds. In sum, these studies provide strong support for the hypothesis that sweet taste perception exists to provide an ability to identify energy-rich sugars.

More recently [8], we conducted behavioral and molecular studies with giant pandas, animals that consume plants, but ones (bamboo) without abundant simple sugars. Would this member of the order Carnivora retain sweet taste perception, or would the absence of a need to find specific plants that taste sweet also result in relaxed selection for maintenance of receptor function? We found that sweet taste perception is fully functional in giant pandas. Although giant pandas thus retain an avidity for sweet compounds, genetic evidence suggests that this species has lost umami taste perception [9], but as yet we know of no behavioral studies verifying this nor do we understand why this may have occurred and how widespread such loss might be.

Although loss of sweet taste seems common for animals that do not consume plants, are there species that have lost even more of the basic tastes? And if so, how can this be interpreted? Based on genetic studies, we [5] and others [10] have reported that many mammalian species that have returned to the sea (e.g., sea lions, dolphins, whales) may have independently lost function for several, perhaps all, taste quality perception. These genetic studies are consistent with anatomy (many of the species do not have identifiable taste cell structures) and behavior (many eat their food whole, without apparently "tasting" it). The factors responsible for this extensive loss of taste function in marine mammals remain to be determined.

In summary, these data dramatically illustrate how plastic the taste system is and, as illustrated through the sweet taste modality, how it has adapted to changes in diet as species evolved. Similar changes are likely in the other taste qualities. For example, it is likely that species differences in the repertoires of bitter receptors reflect different classes of poisons that these species are likely to confront [11]. Species variation in salt taste perception is also likely to be coordinated with diet. For example, it is possible that strict carnivores may not perceive NaCl in the same way as do herbivorous mammals since carnivores' all-meat diet likely provides sufficient Na^+. Finally, as a third example, the human umami or amino acid receptor responds to only a few compounds (glutamate and a few others). However, this receptor acts as a more general amino acid receptor for rodents and other species. These species differences may also be explained by different feeding ecologies although this remains to be determined. Future comparative research will surely reveal many more interesting and important relationships between taste function, food choice, and diet.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

This review was written by both authors. Both authors read and approved the final manuscript.

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REVIEW Open Access

Is fat the sixth taste primary? Evidence and implications

Russell SJ Keast* and Andrew Costanzo

Abstract

Taste is the chemical sense responsible for the detection of non-volatile chemicals in potential foods. For fat to be considered as one of the taste primaries in humans, certain criteria must be met including class of affective stimuli, receptors specific for the class of stimuli on taste bud cells (TBC), afferent fibres from TBC to taste-processing regions of the brain, perception independent of other taste qualities and downstream physiological effects. The breakdown products of the macronutrients carbohydrates (sugars) and proteins (amino acids) are responsible for the activation of sweet and umami tastes, respectively. Following the same logic, the breakdown products of fat being fatty acids are the likely class of stimuli for fat taste. Indeed, psychophysical studies have confirmed that fatty acids of varying chain length and saturation are orally detectable by humans. The most likely fatty acid receptor candidates located on TBC are CD36 and G protein-coupled receptor 120. Once the receptors are activated by fatty acids, a series of transduction events occurs causing the release of neurotransmitters towards afferent fibres signalling the brain. Whether fatty acids elicit any direct perception independent of other taste qualities is still open to debate with only poorly defined perceptions for fatty acids reported. Others suggest that the fatty acid taste component is at detection threshold only and any perceptions are associated with either aroma or chemesthesis. It has also been established that oral exposure to fat via sham feeding stimulates increases in blood TAG concentrations in humans. Therefore, overall, with the exception of an independent perception, there is consistent emerging evidence that fat is the sixth taste primary. The implications of fatty acid taste go further into health and obesity research, with the gustatory detection of fats and their contributions to energy and fat intake receiving increasing attention. There appears to be a coordinated bodily response to fatty acids throughout the alimentary canal; those who are insensitive orally are also insensitive in the gastrointestinal tract and overconsume fatty food and energy. The likely mechanism linking fatty acid taste insensitivity with overweight and obesity is development of satiety after consumption of fatty foods.

Keywords: Fat taste, Fatty acid, Obesity, Taste reception, Chemesthesis

The sense of taste

The sense of taste presumably evolved to inform us about the nutritious or toxic value of potential foods. The primary organ responsible for the sense of taste is the tongue, which contains the biological machinery (taste receptors) to identify non-volatile chemicals in foods and non-foods we place in our mouth. Once a food enters the mouth, the tongue aids in the manipulation of the food, assisting breakdown and bolus formation before swallowing the food. During this critical period of food manipulation, the tongue is sampling chemicals in the food, and when food chemicals activate taste receptors, signals are sent from the taste receptors to processing regions of the brain. The signals are decoded by the brain, and we perceive the taste of the food, which could be one of five distinct qualities: sweet, sour, salty, bitter and umami.

It is perhaps appropriate to classify taste as a nutrient-toxin detection system, with the qualities (sweet, etc.) informing us via an associated hedonic response of suitability to swallow or reject, for example sweet elicited by sugars reflecting carbohydrate, sour elicited by free hydrogen ions (H^+) reflecting excessive acid, umami elicited by glutamate and other amino acids reflecting

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protein content, salt elicited by sodium (Na^+) and other ions reflecting mineral content, and bitter reflecting potential toxins in foods. Excessive bitterness or sourness is aversive and informs that the food in our mouth may cause harm and that the best action is to expectorate, whereas the qualities sweet, umami and salty are all appetitive within a relevant intensity range and inform that the food contains compounds we should ingest, in this case, essential nutrients such as carbohydrate, protein and minerals, respectively. As the taste system has evolved to detect the nutrients or toxins in foods prior to ingestion, it makes sense that fats, an essential energy-dense macronutrient required in limited amounts for energy and nutritional needs, would be detected through taste, as other macronutrients namely carbohydrates and proteins are detected through the tastes of sweet and umami.

Fat taste

Fat taste is an area of increasing interest particularly in chemosensory and nutrition research with the possibility that it may be linked with dietary consumption of fatty foods. The intake and regulation of dietary fats is considered especially important in the development of overweight and obesity, given their high energy density and palatability alongside their ability to promote excess energy intake. The intake and regulation of fats in the obese state appears especially problematic given that obese persons prefer higher fat foods that represent significant portions of the obese diet.

Fat has been classified as a taste as early as 330 BC by Aristotle and many other academics over the centuries [1]. More recently, fat has been associated with texture, flavour release and thermal properties in foods, but not the sense of taste [2]. This may seem like an irrelevant academic point, but the taste system is only activated when a saliva-soluble component of a potential food activates receptors on taste cells. Adding to the importance of the sense of taste is the interplay between taste cell activation and multiple digestive processes, therefore making the link between taste and fat intake very important, especially given the link dietary fat has with the development of obesity.

For fat to be generally accepted as a taste, it must meet five criteria: 1) There must be a distinct class of affective stimuli, and the stimuli responsible for fat taste are the breakdown products of fats and fatty acids [3,4]. 2) There should be transduction mechanisms including receptors to change the chemical code of the stimuli to electrical signal. Emerging evidence suggests that CD36 and G protein-coupled receptor (GPCR) 120 are the most likely candidate receptors on taste bud cells (TBC), with multiple taste transduction mechanisms also involved [5]. 3) There must be neurotransmission of the electrical signal to processing regions of the brain [6,7]. 4) There should be perceptual independence from other taste qualities. This criterion is controversial, and while there is certainly no obvious perception such as the sweetness of sucrose or saltiness of NaCl, some researchers claim less well-defined perceptions for fatty acids [8]. Others suggest that the fatty acid taste component is at detection threshold only and any definable perceptions are associated with either aroma or chemesthesis [4,9]. 5) Finally, there must be physiological effects after activation of taste bud cells.

What follows is a brief summary of evidence supporting fat as the sixth taste and potential relevance of fat taste sensitivity to food consumption and development of obesity.

Fatty acids as stimuli

While it is well established that oxidised or reverted fatty acids or fatty acids at high concentrations are unpleasant to taste, the taste quality of fatty acids will vary according to their concentration in a food. The levels of fatty acids involved in fat taste are low enough not to be considered unpleasant in unspoiled food, yet sufficient to activate putative oral receptors. For example, the concentrations of fatty acids required for detection are within ranges which may be inherently present in edible fresh and processed foods (0.1%–3% *w*/*v*) [10], or perhaps made available through enzymatic hydrolysis by lingual lipase.

Lingual lipase

Lipase enzymes are very important as they break the triacylglycerols (TAGs) down so that free fatty acids can be transduced by cellular pathways. In humans, however, lingual lipase presence remains controversial. Data has suggested that lipolytic activity may be present in humans [9,11], although it is unknown whether sufficient concentrations of lingual lipase are produced and whether this originates from endogenous sources or oral microbes. The presence of lipase does appear to have an influence on fatty acid thresholds with research showing that the addition of orlistat (lipase inhibitor) during testing increased fatty acid thresholds [12]. Overall, the weight of evidence suggests that free fatty acids in fatty foods will be in sufficient concentrations to activate putative receptors on taste cells.

Fatty acid taste receptors and transduction

CD36 transporter

One of the proposed mechanisms of oral fatty acid nutrient detection is via CD36, a fatty acid transporter [13]. CD36 is found in the oral cavity on human taste buds, specifically the circumvallate and foliate papillae [14]. Genetic variants of CD36 have been associated with variation of oleic acid (C18:1) detection threshold [12], providing further evidence for a role of CD36 for fat taste in humans.

G protein-coupled receptors

It has been proposed that CD36 may work together with other possible receptors like GPCRs in a signalling cascade to detect fatty acids [8]. GPCR120 (and possibly GPCR40) are activated by fatty acids initiating peripheral signalling cascade that includes a release of calcium that activates the cation channel transient receptor potential channel type M5 (TRPM5) [15]. GPCR120 has been expressed in the apical portion of types I and II cells from animal taste buds [16,17] and, more recently, human taste buds [8].

Delayed rectifying potassium channels

Delayed rectifying potassium (DRK) channels are known to be implicated in the transduction pathway of a variety of taste stimuli. A study by Gilbertson found that polyunsaturated fatty acids (PUFA) slow down DRK polarisation on the foliate and circumvallate papillae taste cells and therefore allow fat to be detected [18].

Neurotransmitter release

A transduction mechanism that converts the chemical signal to an electrical signal is required to establish the taste component in dietary fat consumption. Previous studies suggested that the general chemoreception pathway starts from the fatty acids triggering the receptor or ion channel and results in the complex cascade that leads to the cell depolarization. The neurotransmitters such as noradrenaline and serotonin (5-hydroxytryptamine (5-HT)) will then be secreted towards afferent nerve fibres which trigger the orosensory perception [19]. Further research is required relating specifically to neurotransmission of fat taste.

Perceptual independence

For all tastants, perception of the taste runs along a sensory concentration continuum (Figure 1). At very low concentrations, fatty acids may be detected, albeit with no taste quality attached, i.e. the concentration is too low to be recognised as a taste [20]. As the concentration increases, e.g. as a result of fat hydrolysis within a food, fatty acids may then be tasted or recognised. Once the concentration of fatty acids is high enough for recognition and supra-threshold, the flavour is generally unpleasant. At the supra-threshold level, it is likely that

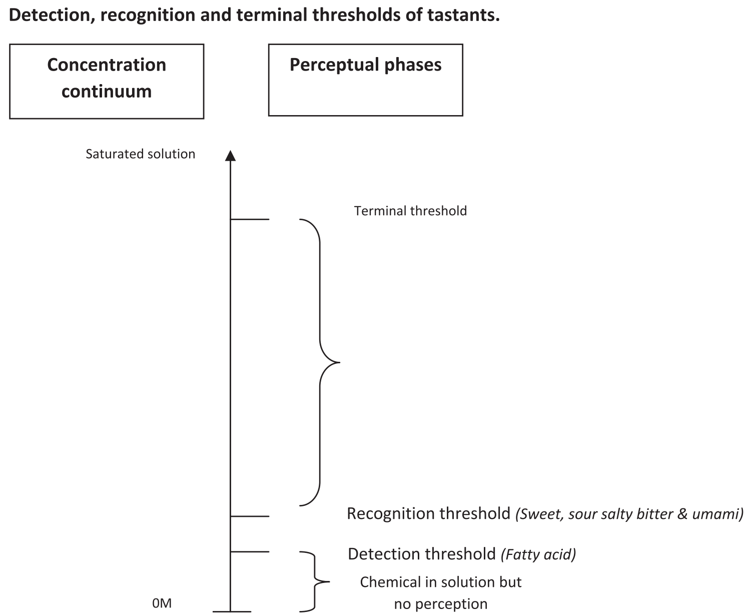

Figure 1 Relationship between chemical concentration, detection threshold and recognition threshold. The left-hand side represents chemical concentration from 0 M solution to a saturated solution. The right-hand side represents the perceptual relationship to increasing concentration and where fatty acid detection is placed in comparison to the five basic tastes.

sensory systems other than taste are involved, for example smell or chemesthesis. Whether there is a recognisable taste quality associated with fat is still up for debate, but there is no doubt that a fat taste quality is not equivalent to easily identified qualities such as sweet or salty. One taste dimension for fatty acids that is reliably measurable is detection threshold, and research has shown that this measure is independent of detection thresholds for other basic tastes, thereby meeting the criteria for perceptual independence [4].

Physiological responses to oral fatty acid exposure

In humans, a 2.8-fold increase in plasma TAG concentrations was recorded in response to oral fat loads. These effects are not observed with sensory-matched fat mimetics, textural cues or smell [21,22], supporting the view that fatty acids activate putative taste receptors that generate an immediate signal which is transmitted to other parts of the periphery, preparing the body for fat digestion and absorption. Additional investigations have also reported fat-specific cephalic phase responses following oral stimulation with fats that include increases in lipase secretion [23]; transient stimulation of gastrointestinal hormones, including cholecystokinin (CCK), pancreatic polypeptide (PP) and peptide YY (PYY) [24,25]; as well as variations in postprandial glucose and insulin [24,26].

Relevance of fat taste to development of obesity

In rodents, differences in fat taste sensitivity appear to influence fat preference, consumption and predisposition to obesity, hinting at a novel role of the taste system in the control of both food intake and weight regulation [27-29]. It has been established that different rodent strains are selectively more or less sensitive to fatty acids and that differences in fat taste are inherently linked to dietary intake and preference.

For example, when wild-type mice were compared to GPCR120 and GPCR40 knock-out mice, the knock-out mice showed an attenuated preference for linoleic acid (C18:2) and C18:1, suggesting that GPCR120 and GPCR40 play a role in the perception of fatty acids [16]. Furthermore, when GPCR120-deficient mice were fed a high-fat diet, they developed obesity and other side effects of metabolic syndrome, indicating a role in regulation of energy intake [30]. Moreover, a high-fat diet reduced expression of CD36 in obese rats which may be associated with fat taste adaptation and also indicates a role in regulation of energy intake [31]. There is also the possibility that CD36 may be involved with the onset of fat-induced satiety [32]. Animal studies have strongly suggested a link between oral sensitivity to fatty acids and development of obesity, with those animals less sensitive to fatty acids unable to adequately regulate intake and overconsuming energy. In other words, the more you taste fat, the less fat you eat.

A feature of the taste system is the large individual differences in sensitivity to compounds [33]. Differential dietary practices amongst obese and lean individuals, especially with regard to fat consumption and preference, are also well established, for example obese individuals have shown a preference for high-fat foods and prefer a greater concentration of fat within specific food matrices when compared to lean individuals [34,35]. Such variations in the taste system along with dietary intake and behaviours have been the focus of recent research studies.

The relationship between oral fatty acid sensitivity, dietary fat intake and body mass index (BMI) has recently been investigated by our group and others [9,36-40]. In general, it was found that those who were more sensitive to the fatty acid C18:1 had lower energy intakes and consumed less total dietary fats and were also better at detecting the fat content of food (custard) [9,37,38]. Another study by Stewart et al. extended these results and also found a relationship in humans between fatty acid sensitivity, food consumption and dietary behaviours, whereby those who were hyposensitive consumed more high-fat dairy products, high-fat spreads and fatty red meat [38]. Conversely, hypersensitive individuals reported behaviours including trimming the fat off meat and avoiding saturated fats [38]. Additionally, various human studies have reported that participants who were classified as hypersensitive to fatty acids also had lower BMIs than hyposensitive individuals [9,38,39,41]; however, other studies have failed to find such associations [37,42]. It has also been reported that fatty acid sensitivity can be modulated by dietary fat, with a high-fat diet causing attenuation of fat taste thresholds in lean individuals, while a low-fat diet results in increased sensitivity to fatty acids [37]. Keller et al. has suggested a possible association between polymorphisms in the CD36 receptor, oral fat perception and fat preference in human subjects [43]. Changes in the preference of high-fat foods have been observed following 12- to 24-week dietary interventions involving fat-restriction, which leads to a decrease in the pleasantness, taste and preference of high-fat foods, suggesting that the experience of fats in foods can be modulated by the diet [44].

The association between fat taste and obesity is probably a result of a coordinated alimentary canal response to dietary fat [45,46] (Figure 2). Indeed, a link between oral fatty acid chemoreception and gastrointestinal tract (GIT) responses to fatty acid has been established with obese individuals having impaired responses to fatty acid in the oral cavity and the GIT [12,37,41,47,48] compared to healthy-weight subjects. The presence of fats in the small intestine in healthy, normal-weight subjects generates potent satiety signals [46]. Gastric emptying is slowed, gut hormones CCK and PYY are released, and ghrelin is inhibited [49,50], altogether causing suppression of energy intake. These physiological satiety

Comparison of satiety feedback after fatty acid chemoreception in lean and obese individuals.

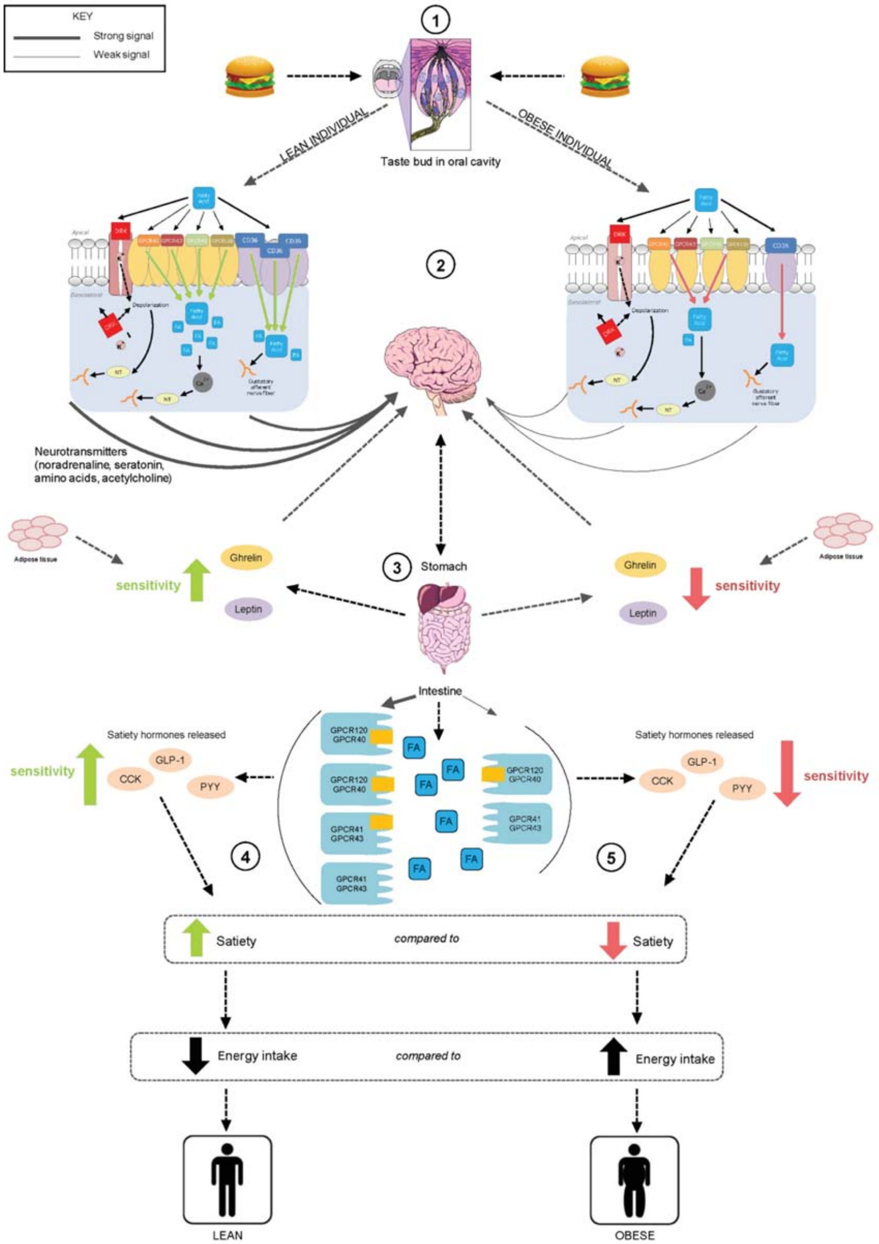

Figure 2 (See legend on next page.)

(See figure on previous page.)
Figure 2 Schematic representation of fatty acid chemoreception in the oral cavity and gastrointestinal tract (alimentary canal) in lean (left) and obese (right) individuals. (1) Fat is present in foods in the form of TAG; free fatty acids are generated during the breakdown of fats and by lipase enzymes in the oral cavity. (2) Fatty acids access putative receptors (CD36, GPCR40, GPCR41, GPCR43, GPCR120 and delayed rectifying potassium (DRK) channels) within taste cells; lean individuals have greater quantities of these receptors compared to obese individuals. The receptors elicit the release of intracellular Ca^{2+} that in turn activates neurotransmitters and hormones associated with the cephalic response. (3) Following fat ingestion, gastric and pancreatic lipase plays a further role in the hydrolysis of fats enabling access to fatty acid receptors on enteroendocrine cells, stimulating satiety hormones and uptake of fatty acids. As a consequence, sensitivity to ghrelin, which is responsible for hunger stimulation, is inhibited, while the satiety-inducing hormone leptin is released as are the hormones CCK, PYY and GLP-1. (4) In a lean individual, expression of fatty acid receptors is greater, therefore increasing fat sensing ability through the alimentary canal and thereby decreasing energy intake. (5) In comparison, obese individuals have decreased expression of fatty acid receptors, attenuating fat sensing ability and increasing energy intake. Reproduced from [52].

mechanisms may be impaired in the obese with subjects voluntarily consuming twice as much energy from fat products as non-obese [41,51]. A recent study illustrated the link between fatty acid sensitivity, fat consumption and satiety. When the population was stratified according to fat taste sensitivity, those who were classified as orally hyposensitive to C18:1 found fat the least satiating macronutrient, while those who were classified as hypersensitive to C18:1 found fat the most satiating. This result was specific for the high-fat meal; this was not observed following a high-carbohydrate, high-protein or balanced meal [36].

Summary

The existence of a sixth taste elicited by the digestive products of fat (fatty acids) is yet to be confirmed; however, a growing body of evidence from humans and other animal species provides support for this proposition. In support for a functional significance of fat taste, differences in taste sensitivity for fat appear to predict certain dietary behaviours, i.e. decreased sensitivity to fat taste is associated with an increased consumption of fat, and this has been reported in both animal and human studies. Moreover, sensitivity to fat can be modulated by the diet, i.e. consumption of a high-fat diet appears to maximise the body's capacity for fat absorption, with no changes in appetite, suggesting that such changes may accompany or encourage excess fat intake and obesity. These data propose a direct role of the taste system in the consumption and preference of high-fat foods, which may be linked to the development of obesity given that differences in BMI have also been linked to oral fatty acid sensitivity. The mechanism allowing for increased consumption of fat is proposed to be via satiety or fullness signals, as associations in both taste and digestive responses to fat have been reported. The next 5 to 10 years should reveal, conclusively, whether fat can be classified as the sixth taste, but no matter what, there appears to be a functional significance to oral chemosensing of fats.

Abbreviations

GPCR: G protein-coupled receptor; TBC: Taste bud cell; TAG: Triacylglycerol; DRK: Delayed rectifying potassium; PUFA: Polyunsaturated fatty acids; CCK: Cholecystokinin; PP: Pancreatic polypeptide; PYY: Peptide YY; GIT: Gastrointestinal tract.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

RSJK conceived of the article and drafted the manuscript. AC helped draft the manuscript and revised it for publication. Both authors read and approved the final manuscript.

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Flavour

OPINION

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Science of umami taste: adaptation to gastronomic culture

Kumiko Ninomiya

Abstract

This paper reviews the points behind the more than a hundred-year delay for the acceptance of umami as a basic taste along with the sweet, sour, salty, and bitter tastes after its discovery by a Japanese scientist in 1908. One of the main reasons for the late recognition of umami taste is the difference in culinary culture between Europe and Japan. Recent collaborative studies with chefs and researchers on traditional soup stocks showed different taste profiles for the Japanese soup stock '*dashi*' and the western-style soup stock. The profile of free amino acids in *dashi,* when compared to the one in the Western style soup stock, explains why umami has been more easily accepted by Japanese who have being traditionally experiencing the simple umami taste of dashi. The recent exchange on cooking methods and diverse types of umami-rich foods in different countries has facilitated a new approach to culinary science blending culinary arts, food science, and food technology for healthier and tastier solutions.

Keywords: Umami, Glutamate, Inosinate, Guanylate, Amino acids, Soup stock

Introduction

Umami is the taste imparted by a number of substances, predominantly the amino acid *glutamate* and 5′-ribonucleotides such as *inosinate* and *guanylate.* After the discovery of umami by Kikunae Ikeda in 1908 [1], almost 100 years were required to obtain a global scientific recognition of umami as one of the basic tastes together with sweet, sour, salty, and bitter. The original idea of researching on glutamate occurred to Kikunae Ikeda when studying physical chemistry in the laboratory of Wilhelm Ostwald in Leipzig, Germany [2]. During his stay in Germany (from 1899 to 1901), he found that there was a quite peculiar and subtle taste common in tomato, asparagus, cheese, meat, etc., which he first experienced in Germany. Ikeda recognized that there were four well-defined taste qualities, sweet, sour, salty, and bitter. However, he also considered the possibility of an additional taste quality, which was quite distinct from the well-known four basic tastes. After returning to Japan and tasting again the traditional soup stock *dashi* made from dried seaweed konbu (*Laminariaceae Bory*), he realized that dashi hold the same taste he had experienced in German foods. As a result, he began a study to identify the key chemical component in konbu responsible for this unique taste. After a long chemical process, Ikeda isolated glutamic acid from konbu. Then, he prepared and tasted glutamate in the form of salts of Na, K, and Ca. His understanding was that glutamic acid should be present almost exclusively as a salt in konbu. The salts of glutamic acid presented a unique taste that he named umami. At the time Ikeda started his research, glutamic acid was not a new amino acid; it had been first isolated from wheat protein by Ritthausen in 1866, and Fischer subsequently reported its taste as sour at first, becoming peculiar and insipid later [3,4]. As a result, Fisher found no reason to study the sensory properties of glutamic acid. Ikeda completed his work in 1908 and he presented a paper 'On the taste of the salt of glutamic acid' at the International Congress of Applied Chemistry which was held in the US in 1912 [5].

In 1913, Ikeda's disciple Shintaro Kodama identified 5′-inosinate (salt of inosine-5′-monophosphate) as the umami substance in dried bonito, which have been also traditionally used for cooking dashi in Japan [6]. In 1957, 5′-guanylate was also shown to elicit an umami taste by Akira Kuninaka and was found to be the major umami substance in dried shiitake mushrooms [7]. Kuninaka

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was the first to explain that the combination of glutamate with 5′-nucleotides, such as inosinate or guanylate, greatly enhances the effect of glutamate and in turn the intensity of umami taste [8]. Today, the phenomena of synergism is widely recognized and practiced worldwide, such as the combination of konbu with dried bonito in *dashi,* or by mixing vegetables and meat or fish in various soup stocks.

Two great inventors in Europe and Japan

After the discovery of umami, Ikeda and Saburosuke Suzuki, an iodine manufacturer, developed in 1909 a new seasoning, monosodium glutamate (MSG), to simply add umami taste, the key taste compound of *dashi*, to a wide variety of Japanese home-cooked dishes [8]. Suzuki's business was to sell iodine extracted from seaweeds as medicine. Ikeda's original idea was to have Suzuki's patronage the extracting of glutamic acid from seaweeds and develop a new seasoning, MSG. However, the contents of glutamic acid in wheat protein is much higher than that in seaweed, so he decided to develop a mass-production process for MSG from hydrolysate of wheat protein. The production process of MSG by Ikeda was quickly patented in Japan, US, UK, and France [9]. Before the discovery of umami, he read a paper written by the first Japanese medical doctor, Hiizu Miyake, claiming that '*good taste promotes digestion of foods*.' Miyake's theory prompted the invention of the new seasoning MSG by Ikeda that could be easily used in the kitchen to improve the taste of home-cooked meals just like salt and sugar. The passion of Ikeda was to improve the nutritional status of the Japanese population.

It is interesting to look into the history of industrial manufacture of soups, which is one of the most basic savory foods in Europe. Julius Maggi [10], a pioneer in the food industry in Europe, produced appliances for roasting and grinding beans to make flour from peas, beans, lentils, etc. His objective was to provide nutritious and flavorful rapid-cooking dehydrated soups for working-class women who lacked the time and money to prepare proper home-cooked soups. In fact, many housewives started working in his factory. He worked with the physician Fridolin Schuler who held the concept of improving the nutritional content of meals for the laboring classes by making packaged foods with a new soup product. The first industrially produced ready-to-use soups based on hydrolysate was introduced in the Swiss market in 1886, followed by various kinds of soups in cubes in 1908. At that time, it was not known that one of the important taste components of these soups was umami.

The two great inventors in the Far East and the West, Ikeda and Maggi, respectively, developed new products with the purpose of improving nutrition at approximately the same time. Each of the two inventors happened to use hydrolysate proteins to produce new products. Ikeda isolated glutamic acid from hydrolysate of wheat protein, but Maggi used a free amino acids mixture based on hydrolyzed proteins from beans. It is evident that these inventions reflect the different food cultures of soup stocks in Japan and Europe. Glutamate is the most abundant amino acid among the only few free amino acids found in the Japanese soup stock made from konbu (Figure 1). On the other hand, there is a variety of free amino acids found in European soup stocks made from meat and vegetables (Figure 2). The taste of Japanese soup stock made from konbu has a clearer umami taste compared to the one of the European soup stock that presents a complicated taste with the mixture of various free amino acids including the umami taste of glutamate.

The long road to the global acceptance of umami taste

As it is mentioned earlier, the first presentation on the discovery of umami was given by Ikeda in 1912 in the USA. The presentation on 'The Umami Taste' by Shizuko Yamaguchi in the International symposium on food taste chemistry, which was jointly organized in 1979 by the American Chemical Society and the Chemical Society of Japan in Hawaii, was an important step to introduce the fundamental concept of umami taste in sensory science as well as the use of 'umami' as a scientific term [11]. After this presentation, many researches started conducting studies on umami taste not only in Japan but also in the USA and Europe within multidisciplinary fields including food science, nutrition, physiology, brain science, etc. Since pure umami by simple aqueous solutions of MSG, IMP, and GMP was difficult to describe, especially for people outside of Japan, there were many discussions on whether umami was a basic taste or not. Gary Beauchamp summarized results of early studies on the use of MSG in foods conducted in the USA. He realized that humans found umami compounds unpalatable when tasted alone, while they improved the taste of foods when mixed with other ingredients [12]. In the First International Symposium on Umami held in Hawaii in 1985, Michael O'Mahony introduced the results of the description on the taste qualities of an MSG solution by Japanese and American subjects. More than 50% of Japanese subjects answered that the taste of an MSG solution was umami, while only 10% of American subjects answered that MSG tasted umami. More than 40% of the American subjects described the taste of the MSG solution as salty and the remaining 10% said that MSG holds an 'indefinite taste' [13]. Since *dashi*, which has a simple umami taste, is the fundamental soup stock used to cook a variety of Japanese dishes, it is easy for Japanese people to associate the taste of MSG solution with the umami taste in *dashi*. In contrast, the perception of a clear umami taste is not common in Western cultures, most likely because

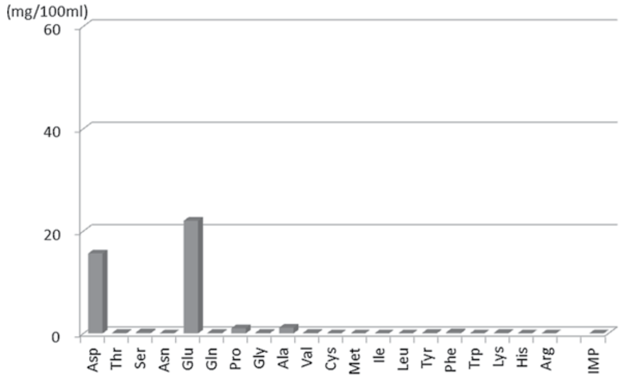

Figure 1 Free amino acids and inosinate in Japanese soup stock 'dashi'. Dashi was cooked based on the recent cooking method introduced by the Japanese chefs' organization in Kyoto. 20 g of rishiri konbu was cooked at 60°C for 1 h [15].

until recently the Western cuisine has not used pure, umami-rich ingredients. Discussion of the key issues pertaining to the establishment of umami as a basic taste lasted until the discovery of human umami taste receptors that was published in 2002 [14].

Recently, umami has spread widely not only in the scientific field but also in gastronomy. Nowadays, cooks and chefs from the culinary arts are able to express accurately the unique characteristics of umami taste using their own words (Table 1) [4]. Trends on collaborative works between chefs and researchers over the past two decades have allowed for blending science and cooking. This has accelerated the deepening and broadening of umami knowledge. It has taken almost 100 years for the global and scientific recognition of umami taste as one of the five basic tastes, but with the support of science and gastronomy, it has become a key element in taste physiology and culinary arts.

The same goal but following a different path

Traditional soup stocks from different countries such as Japanese soup stock *dashi* and Western style soup stocks hold a different taste profile. The cooking of a soup stock consists of extracting a variety of taste substances including umami substances. Free glutamate is one of the major amino acids found in various types of soup stocks, and it is rapidly extracted from food ingredients in the early stages of cooking. Soup stocks in Western

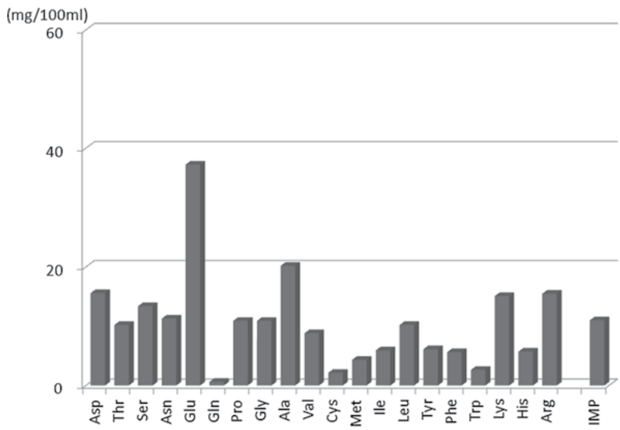

Figure 2 Free amino acids and inosinate in chicken bouillon. Raw materials and preparation of the bouillon were based on the standard method used in the Tsuji Culinary Institute of Abeno, Osaka, Japan [3].

Table 1 Expression of umami by culinary professionals

Savory
Delicate and subtle
Mellow sensation
Earthy, musty, and mushroom-like taste
Taste like a big meaty and mouthful
It makes your mouth water
Mouth watering
Pleasant after taste with satisfaction
Lingering sensation
Subtle and ambiguous
Full tongue and coating sensation
Fullness of taste and that filled my mouth
It provide deep flavor and harmony balance

Ninomiya et al. [3] and Umami Information Center [4].

countries rely on a long cooking process for the extraction and concentration of taste substances from food ingredients such as meat, poultry, or fish, and vegetables. As a result, umami harmonizes with the overall flavor [3]. In Japan, food ingredients that are especially high in umami, such as dried seaweed konbu and dried bonito, are used for cooking the Japanese soup stock *dashi*. Konbu is dried slowly over a long period of time to remove moisture and unfavorable odor, and boiled fillet of bonito is smoked and sprayed with a mold culture (*Aspergillus glaucus*) to make the hardest food in the world. Umami is concentrated in advance in these food ingredients. Because of the unique and long process of making dried konbu and bonito for Japanese soup stock *dashi*, umami can be rapidly extracted during cooking. Thus, cooking time for Japanese soup stock *dashi* is considerably shorter, less than 1 h than in Western soup stock. There are only a few amino acids in Japanese soup stock including glutamate and aspartate. The major amino acids in Western soup stocks are glutamate, alanine, and arginine besides other amino acids [15]. Neither approach is superior to the other; both are different ways of achieving the same goal. Although the free amino acid profile of *dashi* is simpler than Western soup stock, miso, fermented soybean paste, adds a variety of free amino acids in the process of cooking miso soup. It is interesting to note that a proportion of free glutamate and aspartate in the total free amino acid content in miso soup and consommé is quite similar as shown in Figure 3. The proportion of glutamate in relation to the other free amino acids in soups is the same.

Conclusion and future outlook

Using umami taste in a low-salt diet increases the palatability of the foods [16]. Chefs who understand umami taste realized that umami keeps the palatability of dishes even though the concentration of salt is lower than usual. Although there is no scientific data yet to back up the effect of umami in low-fat foods, experiences with chefs suggest that umami compounds may have the ability to improve the palatability of low-fat foods like it does with low-salt foods. Utilizing the taste-enhancing properties of umami to improve the acceptability and palatability of food is beneficial for meals served in hospitals and nursing homes for the elderly [17,18].

The exchange of knowledge on cooking methods and diverse types of umami-rich foods in different countries has made it possible to design new combinations of

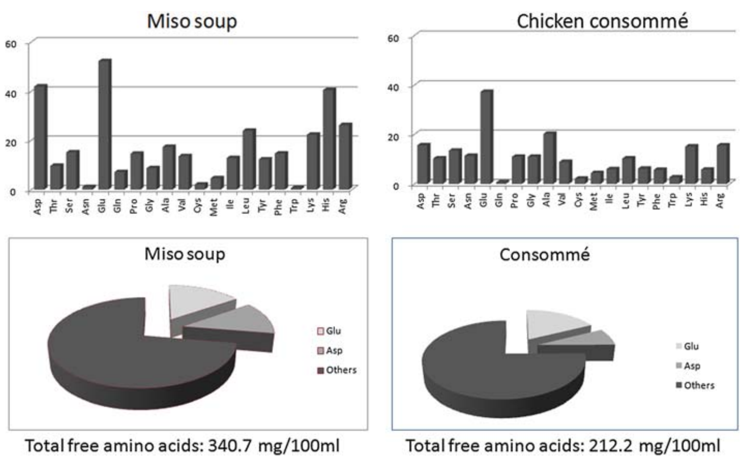

Figure 3 Comparison of free amino acids in miso soup and chicken consommé [15].

ingredients for the creation of a new style of soup stock. Recent studies showed that eating umami-rich foods is helpful to improve the severe condition of dry mouth in elderly people, because umami promotes salivation [19]. The total amount of saliva secretion that results from umami taste stimuli is larger than that by sour taste [20]. There are studies that apply the taste-enhancing properties of umami to improve the acceptability and palatability of meals for the elderly in nursing homes that were conducted in both Japan and the UK [4,21]. The most recent studies on the effect of umami taste on appetite and satiety suggested that adding umami, MSG, and IMP to a high-protein soup enhanced the satiety signal of proteins [22]. These scientific approaches as well as chefs' approach to use umami could not only tackle the challenge of healthy eating, but it could also adapt to the taste preference of every gastronomic culture.

Competing interests
The author declares that she has no competing interests.

Authors' information
Kumiko Ninomiya, PhD is the director of Umami Information Center which is non-profit organization based in Tokyo, Japan.

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SHORT REPORT Open Access

Mechanism of the perception of "*kokumi*" substances and the sensory characteristics of the "*kokumi*" peptide, γ-Glu-Val-Gly

Motonaka Kuroda* and Naohiro Miyamura

Abstract

Some foods are known to have flavours that cannot be explained by the five basic tastes alone, such as continuity, mouthfulness and thick flavour. It was demonstrated that these sensations are evoked by the addition of *kokumi* substances, flavour modifiers that have no taste themselves. However, their mode of action has been poorly understood. During a study on the perception of amino acids and peptides, it was found that glutathione (GSH) was one of the agonists of the calcium-sensing receptor (CaSR). We have hypothesized that CaSR is involved in the perception of *kokumi* substances. We found that all CaSR agonists tested act as *kokumi* substances and that a positive correlation exists between the CaSR activity of γ-glutamyl peptides and *kokumi* intensity. Furthermore, the *kokumi* intensities of GSH and γ-Glu-Val-Gly, a potent *kokumi* peptide, were significantly reduced by the CaSR-specific antagonist, NPS-2143. These results suggest that CaSR is involved in the perception of *kokumi* substances. A potent *kokumi* peptide, γ-Glu-Val-Gly, enhanced sweetness, saltiness and umami when added to 3.3% sucrose, 0.9% NaCl and 0.5% MSG solutions, respectively. In addition, γ-Glu-Val-Gly enhanced the intensity of continuity, mouthfulness and thick flavour when added to chicken soup and reduced-fat cream. These results suggest that γ-Glu-Val-Gly is a potent *kokumi* peptide and would be useful for improving the flavour of food.

Keywords: Calcium-sensing receptor, Glutathione, Thick flavour

Findings

Introduction

Recent developments in molecular biology have demonstrated that the five basic tastes, sweet, salty, sour, bitter and umami are recognized by specific receptors and transduction pathways [1]. However, some foods are known to have flavours that cannot be explained by the five basic tastes alone, such as continuity, mouthfulness and thick flavour. Ueda et al. have previously investigated the flavouring effect of garlic extract that enhanced continuity, mouthfulness and thick flavour when it was added to an umami solution [2]. These authors demonstrated that several sulphur-containing compounds, identified as S-allyl-cysteine sulfoxide (alliin) and glutathione (GSH, γ-Glu-Cys-Gly), were responsible for this effect [2]. Although these compounds have only a slight flavour in water, they substantially enhance the continuity, mouthfulness and thick flavour when added to an umami solution or various foods [3]. They proposed that substances with these properties should be referred to as "*kokumi*" substances. However, their mode of action has been poorly understood. In this study, we aimed to clarify the mechanism of the perception of *kokumi* substances and the sensory characteristics of the potent *kokumi* peptide, γ-Glu-Val-Gly.

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Mechanism of the perception of *kokumi* substances

During a study of a G-protein coupled receptor (GPCR) that perceives amino acids and peptides, we found that GSH was one of the agonists of the calcium-sensing receptor (CaSR) [4]. We have hypothesized that CaSR was involved in the perception of *kokumi* substances. First, the *kokumi* intensity of various CaSR agonists was investigated. It was demonstrated that all CaSR agonists tested, such as Ca^{2+}, protamine, polylysine, L-histidine and γ-glutamyl peptides, enhanced the taste intensity of umami-salty solutions. Second, since GSH (γ-Glu-Cys-Gly) was a potent *kokumi* substance, various γ-glutamyl

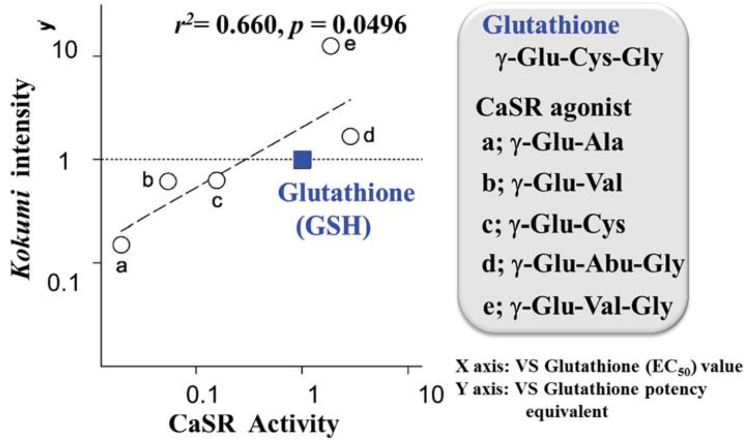

Figure 1 The correlation between the CaSR activity and *kokumi* intensity of various γ-glutamyl peptides. The CaSR activity and *kokumi* intensity were measured by a methods described in [4].

peptides, such as γ-Glu-Ala, γ-Glu-Val, γ-Glu-Cys, γ-Glu-Abu-Gly (Abu: α-aminobutyric acid) and γ-Glu-Val-Gly were synthesized. The CaSR activity of these peptides was measured according the method previously reported [4], and the *kokumi* intensity was measured by sensory evaluation as described previously [4]. The results are indicated in Figure 1, and they reveal that the CaSR activity of γ-glutamyl peptides is significantly and positively correlated to the *kokumi* intensity measured by sensory evaluation ($r = 0.81$, $p < 0.05$) [4]. Thirdly, the *kokum*i intensities of GSH and γ-Glu-Val-Gly, a potent *kokumi* peptide, were significantly reduced by the CaSR-specific antagonist, NPS-2143 [4]. These results therefore strongly suggest that CaSR is involved in the perception of *kokumi* substances. In addition, we tried to investigate the response of taste cells to *kokumi* substances using a slice of mice taste buds. It was demonstrated that certain taste cells responded to the stimulus of *kokumi*

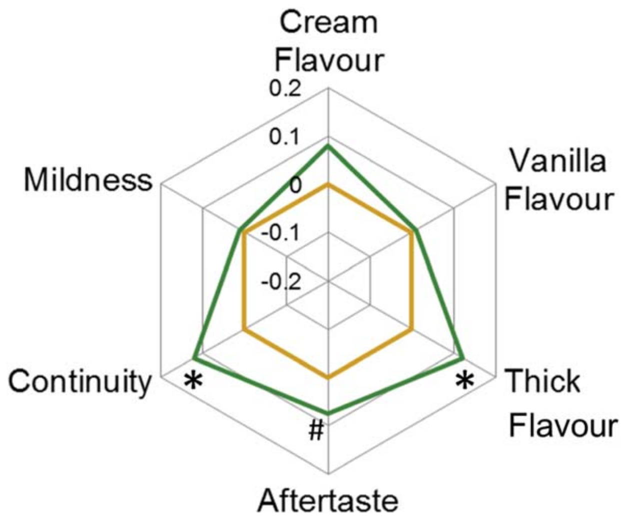

Figure 2 Sensory characteristics of low-fat custard cream with added γ-Glu-Val-Gly. A yellow line indicates the mean scores of the control low-fat custard cream. A green line indicates the mean scores of the low-fat custard cream with 0.004% of γ-Glu-Val-Gly.

substances and this response was significantly suppressed by the CaSR-specific antagonist, NPS-2143 [5]. These results suggest that CaSR in taste cells is involved in the perception of *kokumi* substances.

Sensory characteristics of the "*kokumi*" peptide, γ-Glu-Val-Gly

The kokumi intensity of γ-Glu-Val-Gly was measured by the point of substantial equivalent (PSE) method described previously [4]. The sensory evaluation demonstrated that 0.01% solution of γ-Glu-Val-Gly produced a *kokumi* equivalent to a GSH solution of 0.128%. Therefore, we estimated that the *kokumi* intensity of γ-Glu-Val-Gly was 12.8 times stronger than that of GSH [4]. This result suggests that γ-Glu-Val-Gly is a potent *kokumi* substance.

Next, we investigated the effect of γ-Glu-Val-Gly on the basic tastes (sweet, salty and umami). As results of the sensory evaluation with the trained panelists (n = 20), the addition of 0.01% γ-Glu-Val-Gly significantly enhanced the intensity of sweetness, saltiness and umami [4], although they have no taste themselves (data not shown). These results suggested that γ-Glu-Val-Gly has a property of *kokumi* substances.

In addition, the effect of γ-Glu-Val-Gly on foodstuff was investigated. γ-Glu-Val-Gly was added to chicken consommé soup (prepared from the commercial "Chicken consommé" powder) at a concentration of 0.002%. The sensory evaluation with the trained panelists (n = 20) indicated that the addition of γ-Glu-Val-Gly significantly enhanced the intensity of thickness, continuity and mouthfulness [4]. In the study, thickness was defined as increased taste intensity at ~5 s after tasting, continuity was expressed as the taste intensity at ~20 s and mouthfulness was defined as the reinforcement of the taste sensation throughout the mouth just not on tongue. Furthermore, the effect of γ-Glu-Val-Gly on the flavour of low-fat custard cream (15% fat content; fat in full-fat custard cream is approximately 40%) was evaluated with trained panelists (n = 19). As shown in Figure 2, the addition of γ-Glu-Val-Gly at 0.004% significantly enhanced the intensity of "thick flavour" (thickness of taste; the enhancement of taste intensity with maintaining the balance of taste) and continuity ($p < 0.05$) and tended to enhance the intensity of aftertaste ($p < 0.1$). These results suggest that the potent *kokumi* substance, γ-Glu-Val-Gly, can be used to improve the flavour of various foods. The effect of the peptide on the flavour of various foods is investigated in our laboratory.

Conclusion

In this study, the mechanism of the perception of *kokumi* substances was investigated. All CaSR agonists were *kokumi* substances, and a CaSR-specific antagonist decreased the *kokumi* intensity. Further, the CaSR activity correlated with the *kokumi* intensity. These results suggest that CaSR is involved in the perception of *kokumi* substances. Sensory analyses revealed that γ-Glu-Val-Gly had a *kokumi* intensity 12.8 times stronger than that of GSH and that it enhanced intensities of mouthfulness, thickness (or thick flavour) and continuity of food, suggesting that γ-Glu-Val-Gly is a potent *kokumi* substance.

Abbreviations

γ-Glu-Val-Gly: γ-glutamyl-valyl-glycine; GSH: glutathione; CaSR: calcium-sensing receptor.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

NM designed the construction of this paper. NM and MK collected the data of sensory analysis. MK wrote the manuscript. Both authors read and approved the final manuscript.

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OPINION Open Access

Place-based taste: geography as a starting point for deliciousness

Joshua Evans[1], Roberto Flore[1], Jonas Astrup Pedersen[1] and Michael Bom Frøst[1,2*]

Abstract

Nordic Food Lab (NFL) is a non-profit, open-source organisation that investigates food diversity and deliciousness. We combine scientific and cultural approaches with culinary techniques from around the world to explore the edible potential of the Nordic region. We are intent on broadening our taste, generating and adapting practical ideas and methods for those who make food and those who enjoy eating. This paper describes some of our methods, using geography as a starting point for the exploration of deliciousness, exemplified in our lunch menu served at the Science of Taste symposium in Copenhagen in August 2014.

Keywords: Deliciousness, Geography, Food diversity, Food systems, Nordic region, Food design, Theoretical framework

Introduction

In November 2004, a symposium for Nordic cuisine was organised in Copenhagen at the then newly opened Nordatlantens Brygge, a cultural house for the North Atlantic parts of the Nordic region. Here a group of chefs and food professionals created a manifesto for a new Nordic cuisine that was signed by chefs from Denmark, Faroe Islands, Finland, Greenland, Norway, Sweden and Åland [1]. The symposium and manifesto crystallised a new Nordic food movement that has since developed the regional cuisines of the Nordic countries and territories beyond what anyone could have imagined.

Nordic Food Lab was founded in 2008 in the same spirit, as a research and development lab with the purpose of exploring food in the Nordic region. Chef René Redzepi and gastronomic entrepreneur Claus Meyer, co-owners of the restaurant Noma in Copenhagen, realised that this investigation could not be undertaken in the restaurant kitchen alone. They saw a need for a space where chefs, scientists, and other researchers could come together to investigate raw materials, traditional processes, and modern techniques more deeply than the pressure of daily service would allow. The outcome of the lab's activities was directed primarily towards the development of restaurants, but also with the purpose of expanding knowledge in academic and applied contexts.

Since then, Nordic Food Lab (NFL) has helped to bring science and gastronomy closer together in Denmark [2]. Over the years, we have attempted to shift how chefs and scientists work together, from a simple one-way process of chefs asking scientists to help troubleshoot and solve immediate problems in the kitchen, to a more collaborative effort where research questions are developed and investigated together, integrating different methods and types of expertise. One good example is the work by Mouritsen et al. [3], which explored the use of seaweeds in a Nordic culinary context, and demonstrated how the seaweeds sugar kelp and in particular dulse have great potential as ingredients in the new Nordic cuisine to provide flavour and umami. The interests of the chefs and scientists are diverse and none are experts outside their respective fields, so a true collaborative work brings all parties further than any of them would have managed alone.

The experimental methods used at NFL often resemble those of a design studio with iterations of recipes and as thorough an exploration as possible of the sensory space a particular food can occupy [4]. For this reason, we rely on team members who are capable of dismantling the unnecessary division between science and craft, drawing on knowledge from natural sciences, the humanities and the vast world of diverse culinary traditions.

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Diversity is both our starting point and our goal. It forms a loop of feedback mediated by ecology, necessity, and appetite. There is no single food that can nourish us on its own. The pursuit of good food runs parallel with the pursuit of the biological and cultural diversity upon which truly sustainable food systems rely. Yet infinite choice can be paralysing, and we find creative and investigative freedom in the geographical constraint of our base of our raw materials.

Theoretical framework for deliciousness

In order to create delicious food, it is useful to understand the principles for perception of food and the evaluation of goodness in a food. Creating a new dish or finding a new ingredient to use in our cuisine bears similarities to how we interact with other artefacts of human culture. Looking to theories of human affective response to designed objects or artefacts can thus provide a useful perspective on how similar processes play out in the kitchen and laboratory. Desmet and Hekkert [5] argue that the affective response to a product is a function of three components. First is the immediate perception through our senses, what have previously been termed as the aesthetic experience [6]. Second is the experience of meaning that we ascribe through interpretation and association to assess the personal or symbolic significance of a product experience. The third component in our product experience is the emotional experience that arises from an evaluation of the significance that an experience has for the individual's well-being.

A theory for our interaction with food also needs to take into account the function that food serves for us, the relief of hunger, and the nutritional requirements of our bodies. Norman [7] has formulated that we interact with an object at three distinct levels: First, there is the visceral level, the immediate sensory level. It is how our perception is shaped through the hardwiring of our sensory systems. Second, there is the behavioural level, the function that our interaction with an object serves, such as the needs it satisfies for us. In relation to food, the functional level is the food safety and nutritional aspects, the absence of harmful substances or organisms and the provision of beneficial and necessary nutrients. Third, Norman [7] uses the term 'reflective level' to describe the overall impact a product or object has based on the meaning it gives to us, similar to the meaning level described above by Hekkert and Leder [5]. Figure 1 outlines our interpretation of the three levels of interaction with a food. Here we classify our interaction with food at three overall levels: immediately through our senses, the function the food has, and the reflections we have on the creation of the food.

Perceptual level

We appreciate certain tastes from birth (sweet, fatty, and umami [8]) because they signal the presence of available energy. Appreciation of other sensory properties such crunchy [9] or creamy [10] is learned from positive consequences through conditioned learning and association [11]. Some sensory properties are more dynamic, and their appreciation is a result of the sensory arc that occurs during ingestion, as we chew and swallow. The main purpose of chewing is to comminute, lubricate and subsequently form food into a bolus that can be swallowed without negative consequences, such as inhalation of small particles into the lower respiratory tract [12]. The success of a food from an oral manipulation point of view depends on the efficiency of comminution, lubrication, and bolus formation. The trajectory of this process has been termed the philosophy of the breakdown path [13].

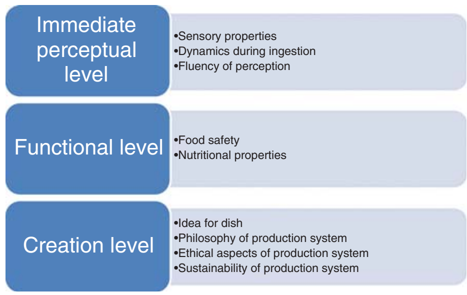

Figure 1 Schematic overview of three levels of food interaction. Overview of requirements for a food to be considered 'good' in different domains.

When we experience foods we implicitly learn some lawful relationship between different sensory properties. For example, we learn to associate the bright orange colour of sea buckthorn with its passion fruit-like aroma and its tangy sourness. After repeated exposures there is fluency in this learnt relationship, which generates intrinsic pleasure as a result of this faster perceptual processing [6]. Gradually, as we become more experienced, our sensory systems can better discern small differences and nuances that in earlier exposures went unnoticed. Gibson [14] suggests that the perceptual development and learning are processes of distinguishing the features of an almost inexhaustibly rich input, hinting at the immense potential to continually develop our senses further. Experienced wine connoisseurs, for example, may be able to distinguish minuscule differences in sensory properties that allow them to correctly identify the vineyard, producer and vintage of a wine and to take great pleasure in analysing and dissecting these sensory inputs of a food.

Functional level

The function of food from a physiological perspective should not be neglected, although it is something that is often taken for granted. Food needs to be safe to eat, i.e.

not cause disease. A good food serves the purpose of providing nourishment, and indeed, the range of intake that provides a person with sufficient macro- and micronutrients is broad. And though nutritional recommendations should be seen as guidelines that can form the basis for nutrition policies, or formulation of diets and foods [15], they are not the be-all and end-all of the complex functionality of food in diets in practice.

Creation level

In relation to food, the parallel to the reflective level or the meaning we ascribe to food is their creation — the production system that brings about the food, or the ideas behind a particular food or dish. A particularly good example of a food that is admired for its idea is Michel Bras' 'chocolat coulant', or chocolate cake with a runny heart that the chef invented in the early 1980s, which for many years has been a signature dish in his restaurant. According to chefs, it is one of the most copied recipes in the world. The ingenuity that was necessary for Michel Bras to develop this particular cake, with a complex preparation that according to legend includes short pieces of a garden hose and freezing the dough before baking, has made it appreciated by his diners for decades, and admired by chefs all over the world. It has helped build Michel Bras' reputation as one of the best chefs in the world (see for instance [16]). Similarly, the artist Olafur Eliasson expresses his admiration for René Redzepi's dish 'Milk skin with Grass', where the grass and the garnishes all originate from the same pasture as the cow that made the milk, and upon which it grazed on, a representation of a particular place at a particular time [17].

A significant part of the appreciation for a food can stem from how it has been created. Several organisations have developed guidelines for goodness in the production system according to their principles. The International Federation of Organic Agriculture Movements (IFOAM) has a set of four principles that form a base for interconnected ethical principles to guide the development of organic agriculture. The four principles are briefly put: health, ecology, fairness and care [18]. The Slow Food movement has a similar succinct statement for their manifesto for good food: good, clean and fair [19,20]. The principles for both these organisations can also be understood in terms of philosophy, ethics and sustainability, as indicated in Figure 1.

These three levels of interaction with a food—perceptual, functional, and creational—help us understand the underlying principles for delicious foods, and can offer explanations for why some foods are indeed delicious.

The menu

Food that excels in the three different domains at the same time is irresistible, as the goodness in the different domains act in synergy with each other. Our pursuit of deliciousness leads us to seek out the delicious potential in as many places and organisms as possible, and often, it is in the neglected, underutilised, forgotten and ignored raw materials that we discover and rediscover unique sources of deliciousness. Similarly, our interest in exploring culinary techniques from both our region and cultures across the world allows us to broaden the culinary potential of these raw materials, by tracing the connections between diverse traditions and translating existing knowledge into our regional context. Combining this biogeographical constraint for raw materials with an openness to all types of knowledge and technique is a starting point for cooking that says something about us and imbues the foods we eat with a connection to this place and this time.

For the Science of Taste symposium, our team developed a menu to both nourish the symposium participants and illustrate how food can be delicious in more than one way. The menu consisted of four dishes served in succession. Figure 2 shows a gallery of images of the different elements of the menu.

Beef heart tartare

We wanted to illustrate the particular qualities of (what are nowadays) underutilised parts of the animal. The heart is a continuously working muscle, which gives it a very different texture than skeletal muscles. Our hearts came from 1-year-old biodynamic calves from Østagergård in Jystrup, Denmark, which we minced while maintaining some structure of the meat. We seasoned the minced heart with black garlic, fresh tarragon, and fig leaf tincture. Black garlic is a product originating in East Asia, and is produced by keeping garlic in a warm environment with little airflow for around 60 days (we seal ours in vacuum bags and keep them at 60°C) [21]. This process denatures the alliinase enzyme responsible for transforming non-volatile alliin into volatile allicin, the pungent sulphurous compound in garlic, especially when its cells are ruptured. Moreover, the low but steady heat creates cascades of low-temperature Maillard reactions, although at a much slower rate than the Maillard reactions commonly experienced in cooking. The finished garlic is characterised by a deep black colour and complex caramelised fragrances.

The tarragon was grown biodynamically at Kiselgården in Ugerløse, Denmark, and provided the freshness to complement the dark richness and acidity of the black garlic.

The Danish island of Bornholm, between Sweden, Germany and Poland at the mouth of the Baltic Sea, has a unique microclimate along its southern coast: soft beaches of fine white sand and an exceptional warmth that lasts later into the fall than is characteristic of the region. This microclimate gives rise to a particular ecology, which includes a robust population of fig trees. In the summer, we made a tincture—a strong infusion of

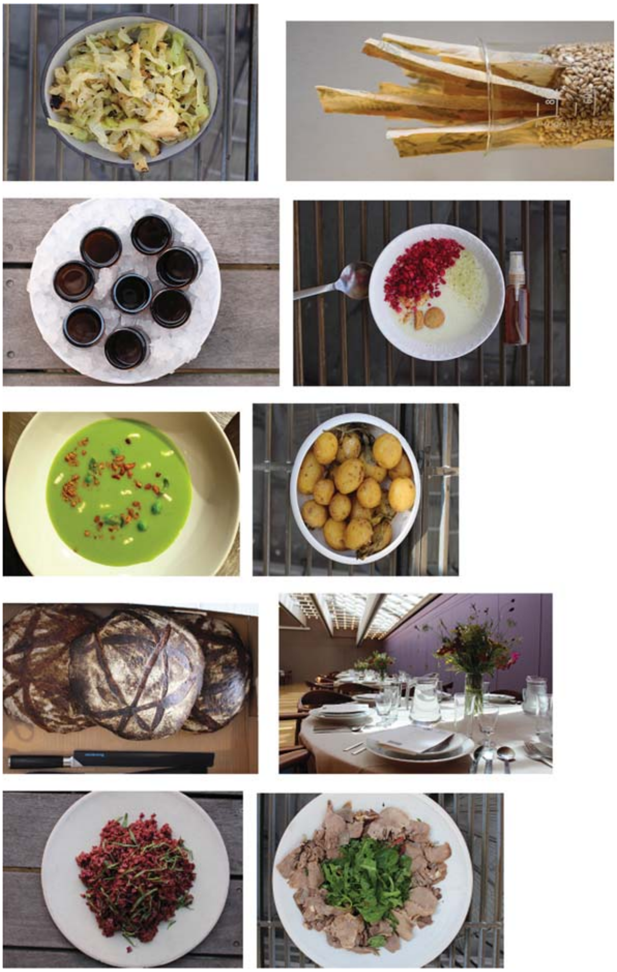

Figure 2 Gallery of the different elements of the menu. Layout of the tables, crispbread, gin, Peas 'n' Bees, sourdough bread, tongue and koji-chovies, potatoes, cabbage, and koldskål.

high-proof ethanol, which has both gastronomic and medicinal applications—from some of these fig leaves, yielding a concentrated source of their characteristic aroma: part coconut and part coumarin (the sweet-smelling compound in tonka bean, woodruff, and sweet clover, among others). A small amount of tincture provided complex herbal top notes, binding the dish together.

We served the dish with a crispbread laminated with wild mugwort and beach roses, and a chilled shot of fragrant, woodsy gin from the island of Hven in the Øresund.

Peas 'n' Bees

This dish emerged from several sources of inspiration. In June 2014, some of our team visited the island of Livø in the Limfjord in northern Jutland to conduct fieldwork for our insect research. While on the island investigating the European cockchafer, we also obtained some fresh bee larvae from a local beekeeper, along with some very mature lovage stems from her garden. As part of an outdoor experimental cookout we steamed the delicate, fatty larvae inside the lovage stems along with jasmine flowers that at the time were riotously in bloom. The herbal and floral notes of the larvae were enhanced in this rustic and simple preparation, and we wanted to take it further in a more controlled context.

One of us (RF) was reminded of a traditional Italian dish that had a comeback in the 1970s called Risi e Bisi, or risotto with peas. The bee larvae visually reminded RF of the rice. The texture of the dish was enhanced with pearled barley boiled in lovage broth, to create a summery, room-temperature soup of creamed fresh peas and lovage, with some blanched bee larvae, fried bee larvae, fresh lovage, and fermented bee pollen to garnish.

Bee larvae are often a waste product of organic bee-keeping, as the drones are removed periodically throughout the summer months as a strategy to lower the Varroa mite population in the hive [22]. They also happen to be extremely nutritious—around 50% protein and 20% unsaturated fats—and their flavour, like honey, can vary according to the local flora and the time of year. All of this makes them a very exciting product to work with in the kitchen. The bee larvae we used in this dish were obtained from a beekeeper in Værløse, outside of Copenhagen, Denmark.

Along with this course, we served large sourdough loaves made with flour from Øland wheat, an old variety of wheat from the island of Øland in Sweden, and virgin butter—carefully cultured cream churned until just before the butterfat and buttermilk separate, yielding a foamy emulsion with a cloud-like texture and bright acidity.

Tongue and koji-chovies

Here again we wanted to showcase the delicious potential of another less-used cut. We cooked the tongues from the same calves (as used above) whole, sous vide for 4 h at 85°C with lots of aromatics. This was followed by 2 h more at 55°C, with butter added. Then, we sliced them and served them slightly warm with lots of fresh greens and herbs and a bright herb sauce. To go along with the tongue, we boiled some new potatoes and tossed them in an umami-rich sauce of koji-chovies (herring fermented in the style of anchovies [23]) and halved pointy cabbage we had grilled and compressed with shio-koji (a mixture of koji, salt, and water, with powerful enzymatic activity) to break it down and bring out its natural sweetness. Both the koji-chovies and shio-koji are excellent examples of translation of technique from other culinary traditions, taking our love of cured anchovies and applying it to a common small fish of the Nordic region, for example, or using the versatility of koji, grain fermented with the fungus *Aspergillus oryzae*, to enhance our fermentation techniques and other processes [24]. The koji, made mainly on rice in East Asia, produces amylases which saccharify the starches allowing the substrate to be further fermented into alcohol (as is the case with sake, or rice wine), along with proteases and lipases which can be further used to break down proteins into amino acids and fats into fatty acids. The enzymatic breakdown of proteins is the main mechanism that gives rise to umami taste in many products, such as soy sauce, miso, and their analogues around East and South-east Asia.

With the main course we served a juice made from Danish apples and seasoned lightly with juniper berries.

Koldskål

We finished with our take on a classic Danish summertime dessert—koldskål. It is a buttermilk soup with a base of egg yolk, traditionally aromatised with lemon zest and vanilla, and served with small cookies called 'kammerjunkere' and sometimes with fresh strawberries. In this version we opted for a more herbal profile, infusing the soup with lemon verbena, and serving with a mixture of freeze-dried lingonberries, raspberries and cranberries, and homemade kammerjunkere topped with lemon thyme sugar.

As this dish was served, we sprayed a finely misted tincture of birch buds over each table, a beautifully resinous and enveloping aroma from this underused part of the tree that conjures up forests of this most Nordic of trees.

We offered this variation on a beloved Danish classic to share the delicious Danish summer with our Danish and international guests alike.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Josh Evans contributed to the writing and editing of the manuscript, and contributed to the development, creation and execution of the menu. Roberto Flore led the development, creation and execution of the menu, and reviewed the manuscript. Jonas Astrup Pedersen contributed to the development, creation and execution of the menu, and reviewed the manuscript. Michael Bom Frøst contributed to the writing and editing of the manuscript. All authors read and approved the final manuscript.

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JE is the lead researcher at Nordic Food Lab, and has a background in the humanities. JE has worked extensively for the last years on food systems and sustainable agriculture. RF is the head chef at Nordic Food Lab. A trained chef, he has focussed in his career on building strong relationships between producers and chefs. JAP is a researcher and product developer at Nordic Food Lab, and has a background in food science, coupled with a longstanding interest in the culinary arts and the restaurant trade. MBF is the director for Nordic Food Lab and associate professor in Sensory Science at University of Copenhagen. He has a background in sensory science, and has worked extensively to connect science and culinary arts to the benefit of both.

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SHORT REPORT Open Access

Temporal design of taste and flavor: practical collaboration between chef and scientist

Hiroya Kawasaki[1*] and Koji Shimomura[2]

Abstract

Background: Recently, many chefs have collaborated with researchers and used scientific techniques in their cooking. These researchers advise chefs from a scientific perspective. However, they do not know what chefs think and what concept they want to express through their dishes. Once scientists understand what motivates chefs in the creation of their new dishes, they would be able to provide chefs with more precise advice.

Findings: The authors identified culinary success factors (CSFs) from context analysis of a culinary magazine for chefs and visualized the relationships between the CSFs when renowned chefs trained in Japanese and French cuisine create new dishes. The results revealed differences not only in cooking techniques, ingredients, and condiments but also in cognitive structure (pattern of thinking) when creating new dishes. One of the authors (KS) has two Michelin stars for his French restaurant. He believes that umami affects the flavor of the main ingredients, which allows him to feature the intrinsic characteristics of the main ingredients. The chef's cognitive structure is apparent in his cuisine.

Conclusions: Based on the results, the chef is advised to understand the nature of umami substances, how to recognize their tastes or flavors, and create a dish that brings flavor changes temporally. In a demonstration, a new dish is unveiled using an umami ingredient according to such a concept, which fits chef's cognitive structure.

Keywords: Chef, Laddering, DEMATEL, Cognitive structure

Findings

Cognitive structures of top chefs

Recently, chefs have become interested in what is happening in the pot when they are cooking [1]. Such chefs have collaborated with researchers and used scientific techniques in their cooking. However, researchers are not usually chefs and do not know what chefs think and what concept they want to express through their dishes. The chef's cognitive structure is thought to be apparent in his cuisine. Once scientists understand what motivates chefs in the creation of their new dishes, they would be able to provide chefs with more precise advice.

Klosse et al. [2] conducted interviews and identified six culinary success factors (CSFs) involved in chefs' development of products (dishes): (1) name and presentation befitting expectations, (2) appetizing smell suitable to the food, (3) good balance of flavor compounds in relation to the food, (4) presence of umami, (5) a mix of hard and soft textures apparent in the mouth, and (6) high flavor richness. Although these factors are important in developing new dishes or improving existing ones, the relationships among them are not clear.

We have recently [3] identified the following CSFs from discussions in monthly articles for professional chefs [4] through the laddering technique: (1) utilization of main ingredient texture, (2) utilization of main ingredient flavor, (3) utilization of main ingredient umami, (4) featured main ingredient, (5) good pairings (complements) between main and secondary ingredients, (6) not too rich, (7) good balance, (8) cuisine more Japanese in style, (9) elegance, and (10) surprise (Table 1). Laddering is a potential interviewing technique for exploring cognitive structures [5]. We also investigated the relationships between

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Table 1 Culinary success factors identified by laddering [3]

	Factors
1.	Utilization of main ingredient texture
2.	Utilization of main ingredient flavor
3.	Utilization of main ingredient umami
4.	Featured main ingredient
5.	Good pairings (complements) between main and secondary ingredients
6.	Not too rich
7.	Good balance
8.	Cuisine more Japanese in style
9.	Elegance
10.	Surprise

The numberings in the table menus were set for visibility.

CSFs in Japanese chefs trained in Japanese or French cuisine by using the Decision-Making Trial and Evaluation Laboratory (DEMATEL) method (Figure 1) [6]. The DEMATEL method consolidates a professional group's knowledge to identify the causal relationships between complicated factors. The comparison of results suggests a difference in type of cuisine affected not only by cooking techniques, ingredients, or condiments but also cognitive structure when creating new dishes.

Cognitive structure-based consultation to chefs

Cooking techniques have been developed for processing the ingredients cultivated locally. For example, chefs of Japanese cuisine have developed techniques for using Japanese ingredients. Today, however, chefs all over the world are connected to each other [7]. They can therefore use the ingredients and cooking techniques of other countries. For example, chefs of Japanese cuisine can use French ingredients such as foie gras and chefs of French cuisine can use Japanese ingredients such as soy sauce.

The umami taste is one of the basic tastes discovered by Japanese scientists, and umami-containing condiments are common in Japan [8]. Although umami does not constitute a key component in classic French cuisine, contemporary chefs of French and other Western cuisines are interested in and understand the concept of umami [9]. Japanese cuisine uses a lot of umami condiments such as soy sauce and dashi made from shaved dried bonito and/or dried konbu seaweed. Japanese chefs have developed a unique technique called *konbu-jime*, which means marinating with konbu seaweed. When raw fish is placed between dried konbu seaweed, the water from the fish is absorbed by the konbu seaweed and the umami compounds of the konbu seaweed move to the fish.

One of the authors (KS), who is a prominent chef in Japan, has a two-Michelin-starred French restaurant. When he was told to use the konbu seaweed for his Iberian pork dish, he mentioned that although he would like to utilize the umami taste of the konbu seaweed, the strong flavor of the konbu seaweed would not be in keeping with the style of French cuisine.

One of the authors (HK) administered the DEMATEL questionnaire to the other author (KS) and analyzed his cognitive structure when he created new dishes. The results revealed that the chef believed that umami affected the flavor of the main ingredients, which allowed him to feature the intrinsic characteristics of the main ingredients (Figure 2). This means that umami is not only one of the basic tastes but also has a strong influence on his dish. This is probably why *konbu-jime* is hard to use for his dish. In fact, as umami (3) influences flavor (2), main ingredient (4), cuisine more French in style (8), and surprise (10) mutually in his cognitive structure, the chef believes that the flavor of the konbu seaweed affects the cuisine more French in style. Thus, in the planning of the Iberian pork *konbu-jime* dish, he was advised to use the umami of the konbu seaweed but remove the flavor of konbu seaweed while leaving the flavor of the pork.

An example of a dish concerning that utilizes the chef's cognitive structure

We provide an example recipe created by one of the authors (KS) for the *Science of Taste* symposium. The

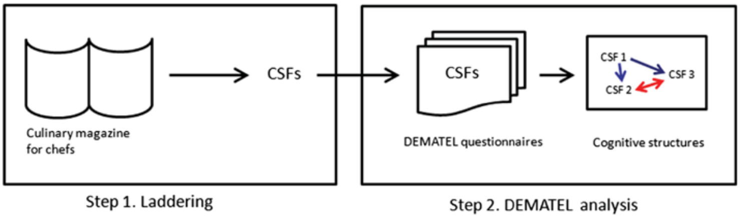

Figure 1 **Scheme for the combination of laddering and DEMATEL method.**

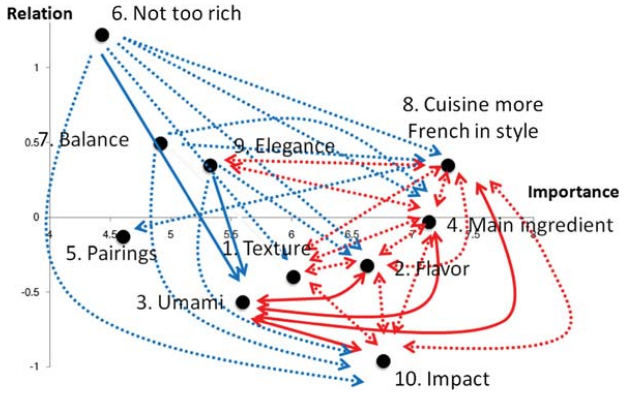

Figure 2 Digraph of chef Koji Shimomura analyzed by the DEMATEL method. The blue arrows are uni-directional, while the red arrows are bi-directional. Solid lines indicate a direct relationship to umami (3), while dotted lines indicate an indirect relationship.

recipe was developed while analyzing the chef's cognitive structure. The photographs of the cooking procedure are shown in Figure 3.

Roasted Iberian pork marinated with dried konbu seaweed

Below are the ingredients of the dish:

180 g of Iberian pork pluma (a type of loin)
25 g of Rausu konbu
8 ml of white wine
10 g of cherry wood chips

Trim the fat from the Iberian pork pluma. Brush the Rausu konbu with white wine. Heat the konbu in a convection oven at 130°C for 2 h to produce the Maillard reaction and smoke the konbu with cherry wood chips. Marinate only one side of the pork with the konbu for 2 days. Sauté the marinated pork in a frying pan and then slice the meat. Garnish with salted black peppers, pickled small onions, and wine-marinated white grapes, and serve.

The umami taste was added to only one side of the pork. When the meat was chewed, the umami taste was released from one side of the meat while the flavor of the pork was released from the other side. The free glutamate concentration of the konbu-marinated surface of the pork was increased after marinating with konbu (Figure 4). The hypothesis of the temporal heterogeneity

Figure 3 Procedure for konbu-marinated Iberian pork.

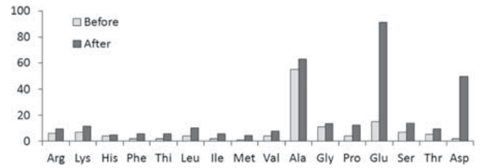

Figure 4 Free amino acid concentration (mg/100 g) of the surface of the pork meat before and after konbu marinating, respectively (analysis by the Umami Information Center).

design of the flavor is shown in Figure 5. We expect that the diner could taste simultaneously the umami and pork flavors but not a strong konbu flavor. Tasting samples were prepared for the audience of the *Science of Taste* symposium.

Conclusions and future outlook

We identified the CSFs from discussion articles in culinary magazines and investigated the relationship among the CSFs, i.e., the cognitive structures of the chefs. We found that there are different cognitive structures for different types of cuisines. In addition, we offered cognitive structure-based consultation to the chef when he created the dish of Iberian pork marinated with konbu seaweed. As the advice for the chef's creation was guided by his cognitive structure, he could receive the advice without discomfort.

Chefs consider a number of complex factors arising from their own cognitive structures when they create new dishes for their customers. Their cognitive structures depend on how they were raised, what circumstances they experienced, and what they would like to express through their dishes. If scientists can understand better how chefs think, there would be mutual understanding between scientists and chefs.

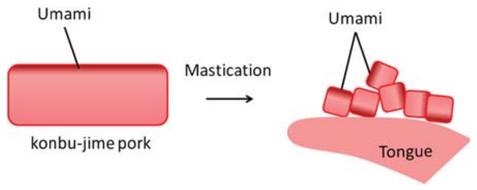

Figure 5 Hypothesis of the temporal heterogeneity design of flavor. After marinating with konbu, the pork was marinated with an umami taste on one side while the pork flavor was retained on the other side. When diners chewed the *konbu-jime* pork, the tongue feels umami with heterogeneity.

Abbreviations

CSF: culinary success factor; DEMATEL: Decision-Making Trial and Evaluation Laboratory.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

HK designed the study, conducted the study of laddering and the DEMATEL method, and wrote the manuscript. KS prepared the tasting dishes. Both authors read and approved the final version of the manuscript.

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Flavour

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Flavours: the pleasure principle

John Prescott

Abstract

Flavour perception reflects the integration of distinct sensory signals, in particular odours and tastes, primarily through the action of associative learning. This gives rise to sensory interactions derived from the innate properties of tastes. It is argued that while the integration inherent in flavours may have adaptive meaning in terms of food identification, the primary purpose is to provide a hedonic value to the odour and the flavour. Hence, flavours may be seen primarily as units of pleasure that influence our motivation to consume.

Keywords: Flavour, Odour, Taste, Sensory integration, Learning, Hedonics

The idea of flavours as the outcome of the integration of tastes, odours and oral somatosensory (tactile) qualities has a long pedigree [1-3]. In recent years, this concept has received support from the identification of the brain's network of neural structures that function together to uniquely encode flavours [4,5]. From the perspective of food preferences, too, flavours seem to be fundamental units. This is primarily because at birth (or in the case of salt, shortly thereafter), we are hedonically inflexible when it comes to basic tastes—sweet, sour, salty, bitter and umami. Our likes and dislikes appear to be pre-set as an adaptive mechanism to ensure intake of nutrients (sweetness, saltiness, umami) and avoid toxins or otherwise harmful substances (bitterness, sourness). On the other hand, there is little evidence that odour preferences are other than the result of experience, a process that may begin in the womb [6].

Of course, we can learn to like or dislike odours in isolation—experience with flowers or sewer smells is sufficient. But in the context of eating, we never experience the odours in flavours without accompanying tastes. This has two consequences. The first of these is that the hedonic properties of tastes become attached to the odour through their repeated co-exposure [7,8], an example of a general associative learning process known as evaluative conditioning [9]. In other words, odours paired with sweetness become liked; odours paired with bitterness typically become disliked. The second process, also based on associative learning, reflects the metabolic value of those food ingredients that give rise to tastes qualities (e.g. sugar, glutamate) or otherwise have value as nutrients (e.g. fat). Odours paired with metabolic value can become liked even when the taste is unpleasant, which explains how we can develop strong preferences for bitter drinks such as coffee or beer, or 'painful' foods that contain chilli. While these two learning processes are seemingly similar, they can be dissociated by, for example, conditioning liking for an odour paired with a non-nutritive sweetener such as aspartame or alternatively pairing the odour with energy in the form of sugar, but under conditions of satiety, in which case the amount of increased liking is limited [10].

Pairing ingested nutrients with odours has other important consequences, particularly in relation to motivation to consume. Thus, pairing novel odours with glutamate in soup increases liking for those odours, but in addition, exposure to the flavour following conditioning also increased feelings of hunger and increased consumption of the soup, relative to simple repeated exposure to the soup [11]. This suggests a mechanism for the development of food 'wanting,' a distinct construct from 'liking' that has been explored in terms of both distinct neural and motivational substrates [12,13]. Wanting reflects a drive to consume, the effects of which can be observed in eating that is independent of energy needs. In particular, wanting can be triggered by sensory cues—odours, visual or auditory cues—that have been associated with nutrient learning. Examples of this can be found in research showing that consumption of a food in response to cues can occur even after consuming the same food to satiation [14]. As such, there is obvious relevance to our understanding of the aetiology of obesity.

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Research evidence for integration of tastes, odours and somatosensory inputs into flavours comes from a variety of sources, including cell recordings in animals [15], fMRI studies of neural activation in humans [16] and psychophysical studies of odour/taste interactions following repeated co-exposure [17]. An important question, though, relates to the adaptive significance of the 'construction' of flavours—why do discrete neural circuits, for example, represent flavours rather than simply odours and tastes separately?

Integration of information from physiologically distinct sensory modalities appears to be a general property of the mammalian nervous system [18]. Moreover, we know from studies of multi-modal sensory integration in other systems (vision, hearing, touch) that such integration, even when it supplies redundant information, aids in the detection and recognition of objects, particularly in those cases where a single sensory modality fails to supply all the necessary information for such recognition [19]. From a theoretical perspective, Gibson [20] has argued that the primary purpose of perception is to seek out objects in our environment, particularly those that are biologically important. As such, the physiological origin of sensations is less important than that these sensations can be used in object identification. Because of its adaptive significance, flavour perception is perhaps the most prominent example of this notion.

But this explanation does not provide a complete understanding of the significance of flavours. While it can be argued that it is taste and odour together that allow us to recognize pear as a pear, in practice, once it is familiar, the pear odour is sufficient. In a world without taste, trial and error would allow one to distinguish pears from apples and could even tell you whether or not pears were safe to eat. However, through learning, the integration of odours with tastes attaches additional meaning to the odour that is primarily hedonic. The pear flavour that is not bitter, not too sour, and quite sweet provides pleasure in eating. In other words, we are motivated to consume it because of its prior associations with the pleasure of sweet taste and the calories that the sweetness, and subsequently, the pear odour signals. And, of course, this occurs even prior to eating: the odour of the pear itself becomes pleasant.

The perceptual consequences of odour/taste integration can be interpreted in the same way. The well-known phenomena of food odours being described in terms of tastes—sweet smell of vanilla or the sour smell of vinegar—are consequences of odour/taste integration and apparently independent from the hedonic changes [8,21]. But these perceptual qualities also have hedonic consequences—sweet smelling odours are pleasant and this quality may in itself motivate consumption even if we cannot identify the actual odour or its source. There is even evidence suggesting that such odours activate the same reward pathways as tasted sweetness [22]. Conversely, a bitter or sour odour is likely to elicit rejection, *especially* if we cannot recognize the odour. As such, these perceptual changes to odours may help compensate for the fact that odour identification is particularly difficult even for common foods [23].

The key purpose of sensory integration is not that it aids identification *per se* (although it might), but rather that it confers a hedonic valence (positive or negative) on to the odour, which crucially is the defining characteristic of the food. Thus, flavours can be most accurately seen as objects constructed for their hedonic qualities. Initial 'gut' responses to foods are almost always hedonic, and this naturally precedes accepting or rejecting the food. Thus, what we perceive when we sit down to dinner are, thankfully, integrated hedonically positive perceptions—*spaghetti al pomodoro* and a nice Chianti—rather than a collection of independent, hedonically diverse tastes, odours and textures.

Competing interests
The author declares that he has no competing interests.

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Flavour

OPINION Open Access

Taste as a social sense: rethinking taste as a cultural activity

Susanne Højlund

Abstract

This article outlines what it means to see taste as a social sense, that means as an activity related to socio-cultural context, rather than as an individual matter of internal reflection. Though culture in the science of taste is recognized as an influential parameter, it is often mentioned as the black box, leaving it open to determine exactly how culture impacts taste, and vice versa, and often representing the taster as a passive recipient of multiple factors related to the local cuisine and culinary traditions. By moving the attention from taste as a physiological stimulus–response of individuals to tasting as a shared cultural activity, it is possible to recognize the taster as a reflexive actor that communicates, performs, manipulates, senses, changes and embodies taste—rather than passively perceives a certain experience of food. The paper unfolds this anthropological approach to taste and outlines some of its methodological implications: to map different strategies of sharing the experience of eating, and to pay attention to the context of these tasting practices. It is proposed that different taste activities can be analysed through the same theoretical lens, namely as sharing practices that generates and maintains a cultural understanding of the meaning of taste.

Keywords: Taste, Tasting, Culture, Practice, Sharing, Context

Taste as a social sense

We eat together. Although there is a constant worry that the sociality of the meal is disappearing, this is rather a myth than reality [1]. Commensality is still highly valued across cultures, even though this value is distributed differently [2]. But stating that eating is a social activity does not in itself explain how taste becomes social or culture becomes taste. As it is not the actual substance of the food that you are sharing, it is still individual what you put into your mouth, what you chew, ingest and perceive. This could lead to the argument that to analyse taste as a cultural phenomenon means, primary, to explore how individuals interpret symbolic meanings of food, e.g. the aesthetic judgement of quality in the Kantian way [3], or how the eater interpret food taboos, definitions and cultural schemes of food rules related to different cultures [4]. But there is still a missing link in explaining how this symbolism becomes a habit or a certain taste preference. The French sociologist Pierre Bourdieu has an influential contribution to this with his concept of *lifestyle* [5] stressing the need to focus not only on ideas and discursive models but also on practice. He explains taste preferences (both the aesthetic judgements and the food choice/other types of consumption) as linked to the distribution of cultural, social and economic capital, and the learning of these preferences as a consequence of social practice [6]. This practice generates a *habitus*, he argues, that guides our choices more or less unconscious. But it leaves us with a rather passive actor [7] and do not enable us to study how one can change taste preferences [8]. Nevertheless it encourages us to see taste as a social sense, as a shared judgement, learned by actively doing taste rather that passively inheriting it from 'culture' [9].

Sharing taste

In order to move the attention from the privacy of the mouth and the subjective, internal reflections to the public space of sharing the experience of eating, it is necessary to develop methodological approaches and models of analyses that can shed light on the social processes of tasting. Many food anthropologists and sociologists are engaged in this kind of analyses focusing on food practices in relation to cultural context e.g. [10,11]. But it is seldom with an explicit focus on processes of tasting. Tasting is part of eating and drinking,

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but not similar hereto. With a focus on tasting rather than on eating, we stress the use of the senses and the judgement of food quality as one dimension of eating. What can be gained from seeing tasting as a practice is a way to understand how ideas of food quality and preferences for certain food stuffs are brought into the social and thereby being object for others and possible to share. I propose, thus, that outlining this field of research would include a mapping of sharing practices, seeing taste not only as something that goes into your body but also the opposite way [8].

From this analytical approach follows that different sharing practices could be studied under the same theoretical umbrella. Such different activities could be: using bodily techniques as e.g. eating with your fingers [12]; intentionally manipulating taste through cooking [13]; talking about taste [14]—from the everyday dialogues in the family to the professional chef's talks on TV [15]; to the writing of food blogs and cook books [16]; using digital media as e.g. sharing food photos at Instagram; arranging food festivals and wine tasting [17]; providing taste education in schools [18] etc. I propose that such different activities can be seen as part of the same social activity: the activity of making taste public [11,19]. Understanding how taste is externalised through culture will make it possible to also analyse how cultural taste preferences are internalised [20]. I am thus pointing to a research field of taste that focuses on the mediated space between food and eater, and an overall research question that asks how this space is constantly created and recreated through cultural mediation [21].

The cultural activity of tasting

I have in this short Opinion outlined what it could mean to see taste as a social sense and stressed that it includes an analysis of tasting as a cultural activity, rather than having an isolated focus on what a product is doing to your taste buds [7]. This is also a shift from taste to tasting. But tasting is not just tasting; tasting means different things in different contexts: The taste of mussels is not the same for a restaurant guest at a gourmet restaurant as for a fisherman in a poor part of the country side [22]. The taste of mussels will be shared in very different ways in these two situations. Mapping strategies of sharing would, thus, not be more than a long list of different types of practices if not the context is taken into account. What a certain taste sharing practice means is related to the situational as well as to the geographical, political and historical context. In order to interpret why people share certain tastes and not others, why they talk about taste in this way and not another etc. one needs to pay attention to the situations and conditions the activity of tasting take place within. This view of senses as cultural is well described, e.g. [23] what is lesser acknowledged is that the cultural activity of tasting has this double function: being both influenced by and influencing the social.

This active use of the sense of taste is difficult to grasp perhaps because the concept of taste itself does not give us many chances to distinguish between different taste situations. It is remarkable how, e.g. the sense of vision has many related words that position the actor in relation to context and activity: you can watch, stare, scan, observe, see, notice, gaze; all these notions express how individuals are using different techniques of seeing [24] in different situations. With these concepts, one can imagine how a person puts his or her sense of vision into play in a social situation—a staring person uses this sense in another way than a person observing or gazing. With the concept of taste we do not—at the moment—have the same different possibilities to conceptualise the act of tasting in relation to context.

One of the ways forward to gain knowledge about how taste and culture influence each other is to explore how the taster is doing the act of tasting in different social situations. This will be a matter of empirical analyses studying the activities and social strategies of sharing taste: from the preparation of tastes to the moment where a taste meets a body—mediated or material—to the study of the contexts this meeting takes place within, and the analysis of which practices of taste sharing are generated under certain circumstances. Taste then becomes an experience that not only goes into the mind of the subject but also contributes to the common creation of knowledge.

Competing interests
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Flavour

SHORT REPORT Open Access

Sensory taste preferences and taste sensitivity and the association of unhealthy food patterns with overweight and obesity in primary school children in Europe—a synthesis of data from the IDEFICS study

Wolfgang Ahrens on behalf of the IDEFICS consortium

Abstract

Background: Increased preference for fat and sugar or reduced taste sensitivity may play a role in overweight and obesity development, but sensory perceptions are probably influenced already during childhood by food cultures and common dietary habits. We summarise the main findings of a large-scale epidemiological study conducted in Italy, Estonia, Cyprus, Belgium, Sweden, Germany, Hungary and Spain. We measured the taste preferences and the taste thresholds in 1,839 children aged 6 to 9 years and investigated factors that might influence the observed preferences as well as their association with weight status.

Findings: Country of residence was the strongest factor related to preferences for sweet, salty, bitter and umami. Taste preferences also differed by age. Regardless of the country of residence and other covariates, overweight and obesity were positively associated with the preference for fat-enriched crackers and sugar-sweetened apple juice.

Conclusions: We conclude that culture and age are important determinants of taste preferences in pre-adolescent children. The cross-sectional data show that objectively measured taste preferences are associated with the weight status of primary school children across varying food cultures. We hypothesise that this association is mediated by an unfavourable food choice as a food pattern characterised by sweet and fatty foods is associated with excess weight gain in these children.

Keywords: Cross-sectional study, Epidemiology, Food culture, Measurement of taste qualities, Overweight and obesity, Sensory taste perception, Bitter taste, Salty taste, Sweet taste, Umami taste

Background

The role of sensory taste perception in childhood obesity

Consumer studies have shown that sensory taste characteristics of foods are important drivers of food choice [1]. Different preferences may lead to distinctive food patterns that in turn may be related to diet-related health outcomes. There is evidence that such food patterns develop early in childhood and adolescence and then carry on into adulthood [2,3]. Few studies on this topic have been conducted in children, and none has employed an international, multicentre epidemiological design. The European epidemiological multicentre study IDEFICS that addressed dietary, lifestyle, social and environmental determinants of children's health created a novel framework for the assessment of sensory taste perceptions of pre-adolescent children. The population-based approach of the study allows the investigation of the determinants of taste perceptions and their association with health outcomes like obesity in childhood [4]. Its prospective design allows for the longitudinal investigation of health outcomes in relation to dietary patterns.

With regard to sensory taste perception, the following research questions were addressed: (1) To what degree

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does sensory taste perception vary in European children? (2) Are taste thresholds or taste preferences associated with food choice or health outcomes? (3) Does new knowledge on sensory taste perception offer new opportunities for primary prevention of diet-related disorders? The cross-sectional analysis of the study shows substantial variation of objectively measured taste preferences and sensitivity across different European countries, indicating a likely effect of different food cultures on the sensory taste perception of children. An increased preference for fat and sugar seems to be associated with overweight and obesity, particularly in girls. Correspondingly, the longitudinal analysis revealed an increased risk for an elevated weight gain in children having a dietary pattern characterised by sweet and fatty foods while this risk was reduced in children with a pattern favouring fruits, vegetables and wholemeal bread. As it seems that dietary preferences are modifiable, preventive efforts may aim at shaping these preferences in a favourable direction already early in childhood.

Methodological approach

The IDEFICS (Identification and prevention of Dietary and lifestyle-induced health EFfects In Children and infantS) study is a multilevel epidemiological study using a European multicentre approach. The study started with a baseline survey of more than 16,000 children who were 2 to 9 years old. It has two main aims, with a strong focus on overweight and obesity in children: (1) To investigate the complex interplay of aetiological factors associated with diet- and lifestyle-related diseases and disorders in a population-based sample of children by means of cross-sectional and longitudinal analyses. A highly standardised protocol was implemented to assess the prevalence of overweight and obesity, related comorbid conditions and major risk factors. Objective measurements of weight status and related health outcomes such as blood pressure, insulin resistance and behavioural determinants such as physical activity are complemented by parent-reported data on diet, social/psychological factors and consumer behaviour. These standardised data allow the comparison of the prevalence and trajectory of health outcomes like childhood obesity and a multitude of risk factors and covariates across a diverse range of European cultures, climate zones and environments represented by eight countries [4-6]. (2) To complement the aetiological approach of the IDEFICS study by a community-oriented intervention programme for primary prevention of obesity in a controlled study design. Here, the study examines the effectiveness of a coherent set of intervention messages to improve diet and physical activity as well as to strengthen coping with stress [7]. The weight status of children was classified according to the age- and sex-specific reference curves of the International Obesity Task Force [8].

We aimed to identify factors associated with taste preference and taste sensitivity. Since sensory testing of free-living children has rarely been done outside the laboratory setting before and because the multicentre design of the study called for a simple and robust method that is not vulnerable to an observer bias, a new method had to be developed and tested for its feasibility and reliability. Based on existing norms like the DIN (German Institute for Standardisation) and long-standing experience with the sensory testing of new food products, a test system was developed under the lead of the Department of Food Technology and Bioprocess Engineering of the Technologie-Transfer-Zentrum Bremerhaven (TTZ). Procedures, substrates and concentrations were tested and adapted in an iterative process with 191 randomly selected boys and girls aged 4 to 7 years from kindergartens and primary schools [9]. It turned out that the taste thresholds of small children are up to an order of magnitude above those of adults. Concentrations of test solutions had to be adapted accordingly.

Since it became obvious that pre-school children wanted to please the examiner by reacting as supposedly desired, the final test protocol was worked out for primary school children aged 6 to 10 years and examiners were trained in avoiding suggestive phrasing of questions or gestures. For optimal standardisation, all stock solutions for the threshold test as well as the juices and test crackers for the preference tests were produced centrally and then shipped to all study locations. A standard operating procedure (SOP) was worked out to ensure standardisation of all tests across study centres and field staff and to minimise measurement bias. Besides the central training of the field staff, the SOP included the following requirements: examiners were advised not to smoke at least 1 h before the test, not to drink coffee or alcohol, not to eat peppermint or strong bubblegum and not to use too much perfume (preferably no perfume at all). Parents had to make sure that the children did not eat or drink (except water) for at least 1 h and that they did not chew peppermint or bubblegum. All materials had to be cleaned with neutral washing liquids free of perfumes.

A random subsample of 1,839 (20.8%) IDEFICS schoolchildren aged 6 to 9 years from Italy, Estonia, Cyprus, Belgium, Sweden, Germany, Hungary and Spain agreed to participate in the sensory taste preference and taste sensitivity tests; 1,705 of them actually provided complete preference data. Tests were usually performed in the morning at the premises of the schools that the children attended.

For the assessment of taste sensitivity, a paired comparison staircase method, i.e. a threshold test, was arranged as a cardboard game where a range of five test solutions were ordered by concentration for each basic taste, i.e. sweet, salty, bitter and umami (in this order). Concentration ranges were as follows: sucrose 8.8–46.7 $mmol^{-1}$, sodium chloride 3.4–27.4 $mmol^{-1}$, caffeine 0.26–1.3 $mmol^{-1}$ and monosodium glutamate (MSG) 0.6–9.5 $mmol^{-1}$. The water-based solutions were offered in small cups (volume 20 ml). Children were asked to act as "taste detectives". They had to find out which of the cups contained pure water and which of them would taste different from pure water. Children were advised to compare each test solution against a reference cup containing distilled water and to put the respective cup on the appropriate field on the board (Figure 1). The lowest concentration at which the child claimed a difference to the reference sample was defined as the threshold concentration. Children were classified as sensitive for the respective taste if their threshold was below the median threshold concentration of the full sample.

The taste preference test was designed as a paired forced choice test using another cardboard (Figure 2). Elevated concentrations of sucrose and apple flavour in apple juice had to be compared with apple juice containing 0.53% added sucrose in a pairwise manner. The amount of sucrose was increased to 3.11% to assess the preference for sweet while 0.05% of commercially available apple flavour was added to assess flavour preference.

Increased levels of fat, sodium chloride and monosodium glutamate in crackers had to be compared against a standard reference cracker. Crackers were heart-shaped and coated with 0.5% aqueous solution of soda lye to make them more attractive. To improve their texture, an emulsifying agent had to be added to the MSG- and salt-enriched crackers. The recipe and its variation for the cracker are summarised in Table 1. The test sequence was as follows: (1) apple juice basic taste versus apple juice with added sugar, (2) apple juice basic taste versus apple juice with added apple flavour, (3) cracker basic recipe versus cracker with added fat, (4) cracker basic recipe versus cracker with added salt and (5) cracker basic recipe versus cracker with added MSG.

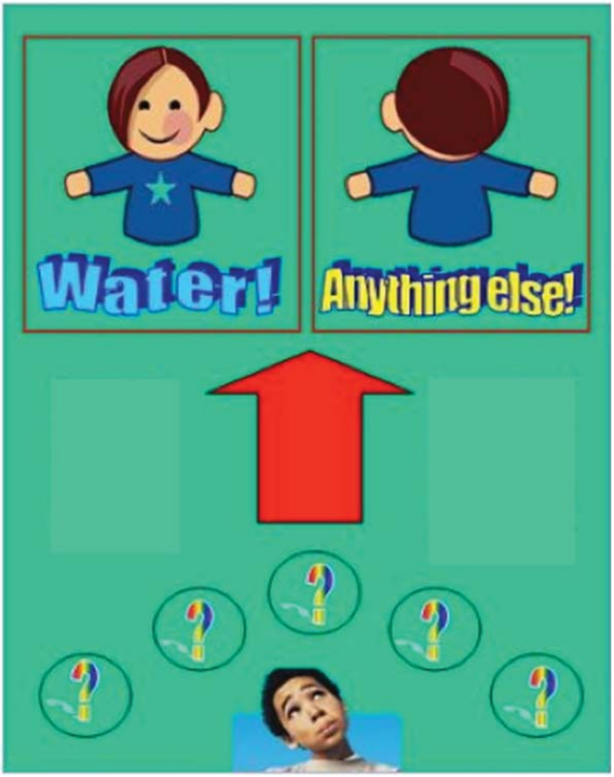

Figure 1 Board game for the taste threshold test. Children were advised to put the tested sample cup on the "water" field if they tasted no difference to the reference sample and on the other field if they indeed tasted a difference.

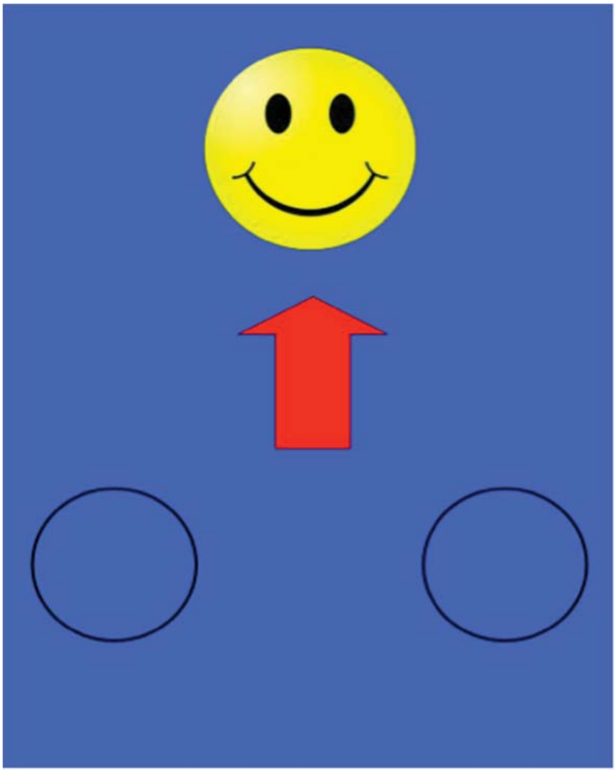

Figure 2 Cardboard used to test the taste preference. Children were advised to put the preferred taste on the smiley.

A parent or guardian living with the child filled in a proxy questionnaire to record age, sex, country of residence, parental education and feeding practices including breastfeeding, first introduction of fruit, TV exposure and using food as a reward or punishment. To report on the usual frequency of the consumption of selected food items and on dietary habits, parents completed the Children's Eating Habits Questionnaire [10,11]. The latter provided the basis for the identification of the actual dietary patterns by principal component analysis [12].

The statistical analysis included chi-square tests to assess differences by survey centre. Odds ratios and their 95% confidence intervals were calculated by a logistic regression analysis to identify predictors and correlates of a preference for sweet, fat, salty and umami taste. Age, sex, parental education, survey centre, breastfeeding and age at introduction of fruits were included in the statistical model as possible causal predictors of taste preferences. TV use, using food as a reward and taste sensitivity were considered as correlates because the direction of an association with taste preferences would not be clear in a cross-sectional analysis like ours. For example, if taste sensitivity is modifiable by environmental factors or dietary behaviour rather than being a stable, genetically

Table 1 Recipe of the cracker to determine fat, salt and umami preference

Type of cracker	Flour/water (%)	Salt (%)	Fat (%)	MSG (%)	DAWE (%)
Reference	91.3	0.7	8	0	0
Salt	89.4	*1.6*	8	0	1
Fat	81.3	0.7	*18*	0	0
Umami	89.3	0.7	8	*1*	1

DAWE diacetyl tartaric ester (emulsifying agent), *MSG* monosodium glutamate.

determined trait, then it may well be that preferences influence preferences and vice versa. Additional analyses were stratified by survey centre where odds ratios were only adjusted for age, sex and parental education. To account for multiple testing, a Bonferroni adjustment of the significance level was done.

Statement of Ethics

We certify that all applicable institutional and governmental regulations concerning the ethical use of human volunteers were followed during this research. Approval by the appropriate Ethics Committees was obtained by each of the 8 centres doing the fieldwork. Study children did not undergo any procedures unless both they and their parents had given consent for examinations, collection of samples, subsequent analysis and storage of personal data and collected samples. Study subjects and their parents could consent to single components of the study while abstaining from others.

Findings

Prevalence of sensory taste sensitivity and sensory preferences

The prevalence of taste sensitivity differs substantially between countries for each of the four basic tastes. The sensitivity for all tastes tends to be generally below average among children from Cyprus. The highest prevalence values were observed for sweet sensitivity in Italian and Estonian children, for bitter sensitivity in Hungarian and Spanish children and for umami in Hungarian children. The prevalence of salt sensitivity varied less between most countries; only in children from Cyprus and Belgium the corresponding prevalence was clearly below the average (Figure 3).

Regarding sensory preferences, most children preferred the food sample with the added flavouring substance for sweet, fat and salt (Figure 4). However, only 34% of the children preferred the cracker with added MSG on the natural cracker. The preference for the added ingredient tends to be generally higher in Hungarian, Spanish and Estonian children. The preference prevalence varies substantially between countries, particularly for fat and umami. The preference prevalence for umami is more than twofold higher in Estonia and Spain as compared to Cyprus and Belgium while the preference for fat is almost twice as high in Estonia and Germany as compared to Cyprus. The preference for the salty cracker is highest in Estonia and lowest in Cyprus and Italy. Sweet preference shows the smallest variation by country, with the lowest prevalence values in Germany and Cyprus. Taste preferences were not significantly associated with each other with the exception of fat and umami. Children preferring the fat-added cracker also had a tendency to prefer the sugar-added apple juice, but this association was only weak and statistically non-significant.

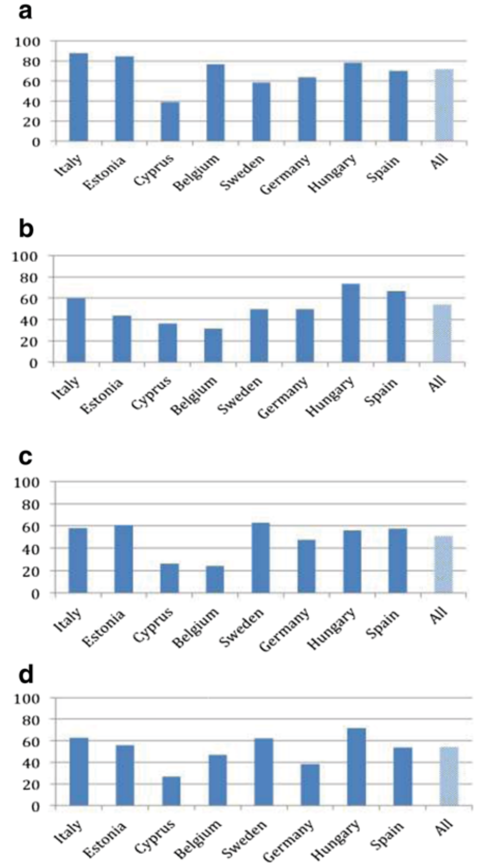

Figure 3 Proportion of children sensitive to four basic taste qualities by country. (a) Sweet sensitive, **(b)** bitter sensitive, **(c)** salt sensitive and **(d)** umami sensitive.

Correlates and consequences of sensory taste preferences

Country of residence is the strongest factor related to preferences for all four taste qualities. No sex differences are observed for any of the taste qualities, but taste preferences differ by age. While the preference for sugar-added juice seems to increase by age, the fat-added cracker is less preferred in 8- to 9-year-olds as compared to 6-year-old children. Also, the preference for salt increases with age while it decreases for MSG. Parental education, early feeding habits, TV viewing, using food as a reward and taste thresholds were not consistently related to taste preferences [13].

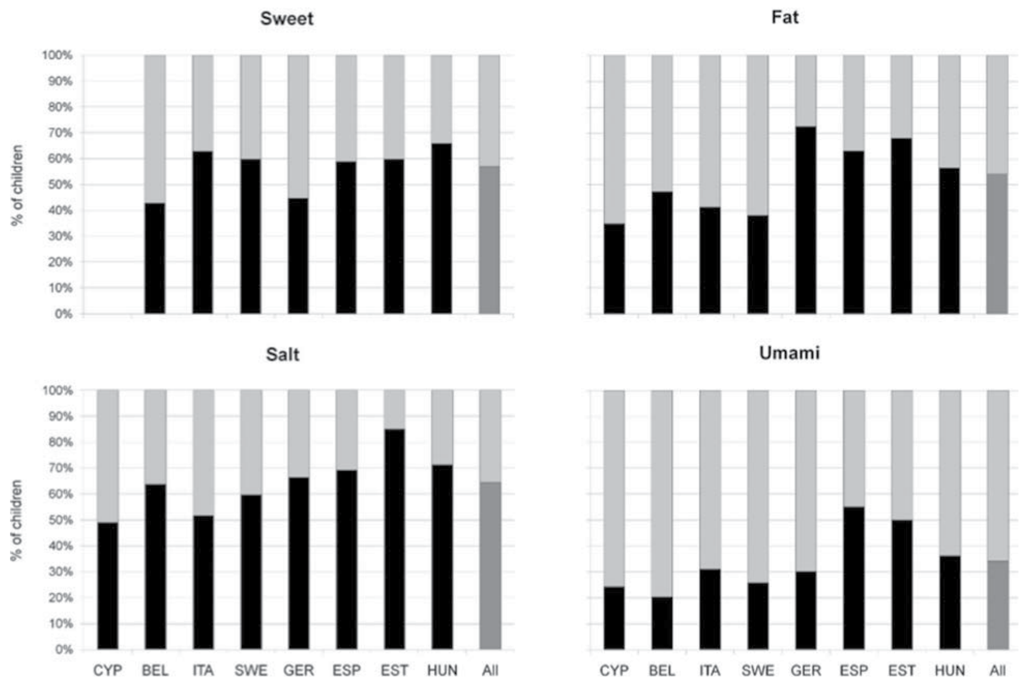

Figure 4 Proportion of children preferring sweet/fat/salt/umami by country.

We also investigated the association between taste preferences and dietary patterns. Children's consumption frequency of fatty and sweet foods was obtained from the food frequency questionnaire (FFQ) completed by a parent for his/her child. Frequent consumption of fatty foods shows an association with fat preference in bivariate analyses, but adjustment for country attenuates this association. No such association is observed for sweet preference and the parent-reported consumption of sweet foods, neither in crude nor in adjusted analyses [14]. Although the reliability of the FFQ was reasonably good [11], the absence of strong associations between objectively measured taste preferences and parent-reported food consumption frequencies may be explained by misclassification of proxy-reported food consumption as indicated by the non-negligible degree of within-subject variation between repeated reports [11].

Weight and height of the children were measured according to highly standardised procedures. Regardless of the country of residence, age, sex, parental education and parental BMI, overweight and obesity were positively associated with preference for fat-enriched crackers and with sugar-sweetened apple juice. The odds of being overweight or obese are elevated by 50% among children preferring the fat-added cracker as compared to children preferring the natural cracker (Figure 5). Children preferring the sugar-sweetened juice also show 50% higher odds of being overweight or obese as compared to children preferring the natural juice (Figure 5). Fat preference associations were stronger in girls. Girls but not boys who simultaneously preferred fatty crackers and sweetened juice reveal a particularly high probability of being overweight or obese [14]. Preference for salt, MSG or apple flavour does not seem to be associated with weight status.

Although the direct association between taste preferences and reported frequency of corresponding food items was relatively weak, we hypothesise that the observed positive association between sensory fat and sweet preference and weight status in our children may be mediated through a corresponding food choice pattern. This hypothesis is supported by the analysis of observed dietary patterns in relation to weight gain. Using a principal component analysis, we were able to identify four distinct dietary patterns [12]: (1) "Snacking" is characterised by the consumption of sandwiches (including hamburgers, hotdogs and kebabs); butter or margarine on bread; snacks, savoury pastries, fritters; snacks, chocolate, candy bars; and white bread, white

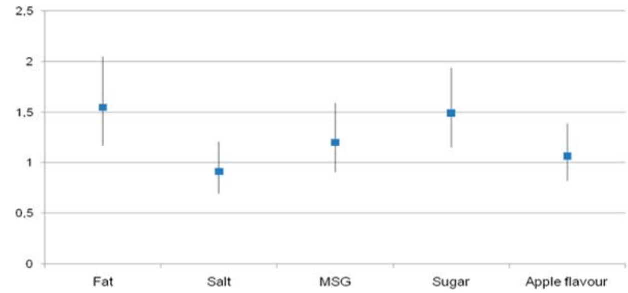

Figure 5 Odds ratios and 95% confidence intervals adjusted for age, sex and country for overweight/obesity in children with preference for added fat, salt and MSG in crackers and for added sugar and apple flavour in apple juice. Natural cracker and natural apple juice served as the reference categories, respectively.

rolls, crispbread. (2) “Sweet and fat” is characterised by the consumption of chocolate- or nut-based spreads; biscuit cakes, pastries and puddings; sweets/candy; fried meats; and soft drinks. (3) “Vegetables and wholemeal” is characterised by the consumption of raw vegetables; wholemeal bread; cooked vegetables; fresh fruit without added sugar; plain milk (not sweetened); and porridge, muesli (not sweetened). (4) “Proteins and water” is characterised by the consumption of fresh fish (not fried); water; fried fish, fish fingers; eggs (fried, scrambled), fresh meat (not fried); and pasta, noodles, rice. During a 2-year follow-up, those children adhering to the “sweet and fat” pattern (upper tertile) had a 17% increased risk for an excessive weight gain while this risk was reduced by 12% in children following the “vegetable and wholemeal” pattern (upper tertile) (Figure 6).

In another approach, we calculated the propensity of children to favourably consume sweet or fatty foods in order to investigate the association between overweight, TV consumption and the adherence to an unhealthy food pattern [15]: The weekly consumption frequencies of each of 17 foods and beverages that are high in fat and of 12 foods and beverages with high sugar content were calculated for each of these categories. The other 14 items of the FFQ were also converted into weekly frequency scores. A continuous propensity score was calculated by dividing the total weekly frequency for the high-sugar or high-fat items by the individual’s total consumed food frequencies. These propensity scores were meant to reflect the proportions of sugary and fatty foods in the whole diet of a child. Dietary fat propensity was calculated as the ratio of fried potatoes, whole fat milk, whole fat yogurt, fried fish, cold cuts/sausages, fried meat, fried eggs, mayonnaise, cheese, chocolate- or nut-based spread, butter/margarine on bread, nuts/seeds/dried fruit, salty snacks, savoury pastries, chocolate-based candies, cake/pudding/cookies and ice cream to total frequencies/week. Sugar propensity was calculated as the ratio of fruit with

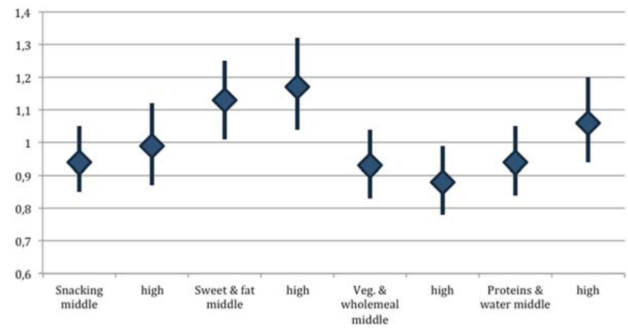

Figure 6 Risk of increased BMI *z*-score (+20%) over 2 years of follow-up by food pattern. Odd ratios (OR) with 95% confidence intervals from mixed effects logistic regression with country as “random effect”, adjusted for sex, age, hours of physical activity/week (continuous), country specific income (low, low/medium, medium, medium/high and high). The lowest tertile of each pattern was used as the reference category; middle = second tertile and high = upper tertile.

added sugar, fruit juice, sugar-sweetened drinks, sweetened breakfast cereals, sweetened milk, sweetened yogurt, jam/honey, chocolate- or nut-based spread, chocolate-based candies, non-fat candies, cake/pudding/cookies and ice cream to total frequencies/week. These two propensity scores were divided into quartiles to assess their association with children's TV consumption using odds ratios. This analysis shows that the propensity of children to consume foods high in fat or sugar is positively and steadily associated with indicators of frequent TV consumption (Figure 7). At the same time, these indicators are associated with a 20% to 30% increased risk for being overweight or obese [15]. We may speculate that a higher exposure to TV programmes—and consequently to food advertisements that mostly promote unhealthy foods—could influence dietary patterns of children in an unfavourable direction. The observed association of high TV consumption with, both, overweight and an unfavourable propensity to consume sugary and fatty foods may indeed provide a starting point for the primary prevention of childhood overweight.

Conclusion

We conclude that culture and age may be important determinants of taste preferences in children younger than 10 years of age. Fat and sweet taste preferences show a positive association with weight status in European children across regions with varying food cultures. The propensity to consume foods with a high content of fat and sugar is associated with indicators of high TV consumption that in turn is more prevalent in overweight and obese children. These associations are based on a cross-sectional analysis, and conclusions about causality of the

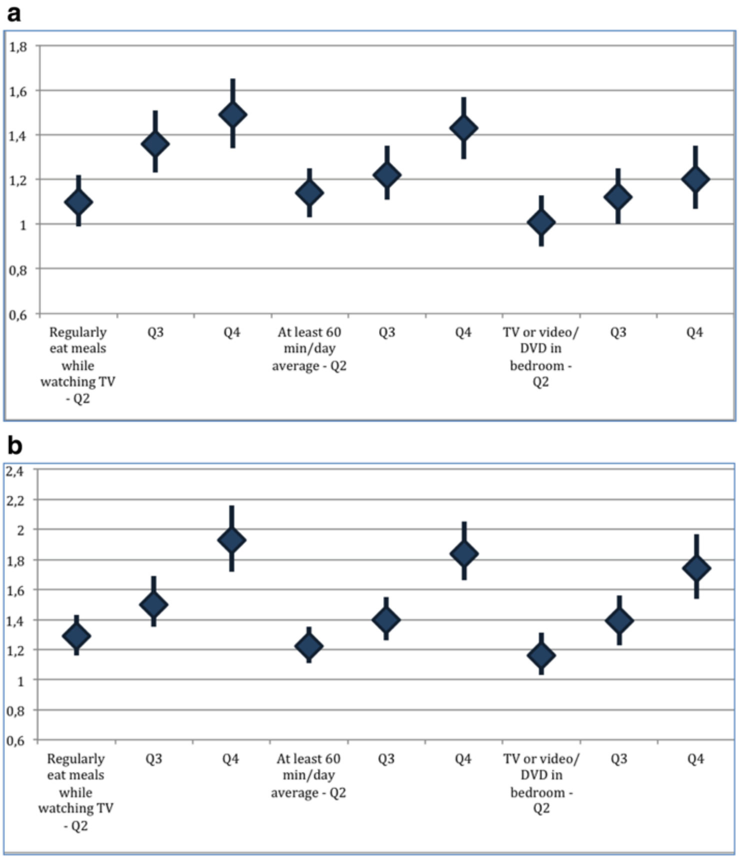

Figure 7 Relation between fat and sugar propensity (quartiles, Q1 = low and Q4 = high) and television habits. Prevalence odds ratios (95% CI) adjusted for age, sex, survey centre and parental education. The lowest propensity quartile (Q1) serves as the reference category. **(a)** Fat propensity and **(b)** Sugar propensity.

associations should thus be drawn with great caution. Nevertheless, the data presented are in agreement with the hypothesis that preference for sweet and fatty foods parallels a higher propensity to consume these foods. The positive longitudinal association of an unhealthy food pattern characterised by sweet and fatty foods with an unfavourable weight trajectory in children provides evidence for a causal relationship. Thus, it seems plausible that food preferences of children are shaped by cultural, behavioural and environmental factors including exposure to TV and other media. Ultimately, unfavourable preferences may result in less favourable food patterns which then lead to negative health outcomes like obesity.

Abbreviations

DAWE: diacetyl tartaric ester; FFQ: food frequency questionnaire; MSG: monosodium glutamate; TTZ: Technologie-Transfer-Zentrum Bremerhaven.

Competing interests

The author declares that he has no competing interests.

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Flavour

OPINION

Open Access

Taste and appetite

Per Møller

Abstract

In this short paper, I discuss two interpretations of the implications of food reward for healthy eating. It is often argued that foods that are palatable and provide sensory pleasure lead to overeating. I discuss an example of an experiment that claims to demonstrate this, to many people, intuitively reasonable result. I point out a number of assumptions about reward and eating behaviour underlying this sort of thinking and ask whether overeating might not instead, to a large extent, result from avoiding reward and sensory satisfaction. Four different experimental results that support the suggestion that 'quality can replace quantity' are briefly reviewed.

Keywords: Taste, Appetite, Overeating, Reward, Sensory pleasure

Humans eat foods, not nutrients. Homeostatic appetite mechanisms based on nutrients are therefore not sufficient to explain human food behaviour. Also, if homeostatic mechanisms were the only determinants of food intake, the recent problems of overeating and obesity would be hard to explain. Other control systems of ingestive behaviour and energy balance have therefore been identified [1]. These systems deal mainly with motivational, cognitive and emotional aspects of eating behaviour. Rewards derived from eating figure strongly in these extensive neural networks. Sensory pleasure from the taste of foods is therefore a major determinant of food intake.

Eating is initiated when a state of hunger is reached, but under most circumstances, not just any food will do; usually, people experience hunger for particular foods under particular circumstances.

Since foods provide reward [2], it is important to understand the processes of hedonic eating [3,4] and in particular, how these processes interact with homeostatic mechanisms controlling energy balance [1].

In this paper, I will discuss two interpretations of the implications of food reward for healthy eating.

Pleasure comes in different disguises: as the immediate sensation of wanting and liking a food when it is eaten or as a longer lasting feeling of well-being after a meal. Berridge and his coworkers have proposed a model of reward based on liking, wanting and learning [2,5]. Liking has been studied very much, despite its inability to predict very much of people's food behaviour [6]. Motivational processes of wanting and desire seem to change more during a meal and to be better able to predict behaviour [7]. Obviously, pleasure derived from a meal also depends on expectations *prior* to eating it and on bodily and mental satisfactions and well-being experienced *after* a meal. These are problems that are virtually untouched by scientific investigation. We need to devise new methods of quantifying pleasure and satisfaction. These methods will probably have to rely on measurements of different types of memory and on measurements of interoceptive states [8].

Optimally, the foods we eat should be perceived as appetitive, not just as filling. Will high gastronomic quality of foods consumed on a daily basis leads to overeating, thereby exacerbating problems of overweight and obesity? This view has indeed surfaced in certain scientific circles [9-11]. It might, to some, seem almost self-evident, but to others, like myself, not at all so. From highly unscientific introspection and conversations with friends and colleagues about these matters, it seems that most of us eat far less of high-quality Parmesan cheese when it is offered, than of cheap, not so tasty hard cheeses. The same applies to wines and chocolate and all other types of food. Very few people can eat a whole 100 g bar of Valrhona chocolate in one go but easily perform this feat with chocolate of a lesser quality. From a more epidemiological point of view, one would wonder why the obesity problem in France is less severe than in other affluent countries with foods and meals generally of a lower quality than those served in France [12]. Many scientists have argued that

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increased pleasure and variety lead to overeating. There is probably little doubt that sensory-specific satieties guide us to eat meals which contain different tastes and textures and this is one of the nature's tricks to help us eat diets balanced in macro- and micro-nutrients without needing to know anything whatsoever about nutrition science [4,13,14]. On the other hand, experiments with real meals under ecologically valid circumstances, as opposed to the often very artificial arrangements and foods subjects face in laboratories, suggest that 'liking' *per se* does not predict when a meal ends [6]. Nevertheless, many workers claim to have demonstrated that pleasure and high variety are important factors for overeating. One example of this kind of thinking is demonstrated in a recent paper by Epstein and coworkers [9].

Epstein et al. randomly assigned 16 obese and 16 non-obese women (aged 20–50 years) to receive a macaroni and cheese meal presented 5 times, either daily for 1 week or once a week for 5 weeks. They also claim to have measured 'habituation' to the food stimuli. Habituation to a stimulus is an expression of the decrement in behavioural and physiologic responses to a stimulus, often observed when repeatedly presenting the same stimulus over and over again. Habituation is an attentional effect that does not involve sensory adaptation/fatigue or motor fatigue. Epstein et al. interpret it differently, describing habituation as a form of learning. Referring to previous work by themselves and others that investigated short-term habituation in their use of the term, the question they ask in this paper is whether there is such a thing as 'long-term' habituation to food.

Whether or not any *effects observed on intake* are causally related to 'habituation' is interesting, but not crucial to potential applications of results like these in the design of meal schemes. The results of the experiment showed that for both obese and non-obese women, daily presentation of a bland food resulted in faster habituation and less energy intake than did once-weekly presentation of the bland food. The smaller energy intake in the once-a-day condition was not *very* significant and might very well have resulted from a serious design flaw of the experiment. Nevertheless, the authors conclude that, if you are offered the same (bland) meal on 5 consecutive days, you will consume less of that particular meal on day 5 than you will on the fifth encounter if you are only offered the (particular) meal once a week for 5 weeks. This result led Epstein et al. to suggest that '*reducing variety may be an important component of interventions for obesity. Habituation may provide a mechanism for the effects of variety on energy intake, such that within-session habituation during a meal can lead to reduced intakes with reduced variety of foods*' [9].

This experiment was considered so important by the editors of the American Journal of Clinical Nutrition that it prompted an editorial written by Nicole M Avena and Mark S Gold [10]. Avena and Gold are fascinated by this work and write.... '*The findings of Epstein et al. provide support and guidance in developing dietary advice, such as the suggestion that people try to eat the same food each day, in which case habituation may develop that would reduce the likelihood of overeating and subsequent obesity*'.

And further... '*Thus, the work of Epstein et al. is important to consider in contemplating and designing meal plans in our variety-rich environment. Clearly, school-lunch planners and public health officials should note that diversity in the menu is not necessarily a virtue, and in fact it may be associated with promoting excess food intake and increased body mass index*'.... In summary, it is suggested that we should '*try to eat the same food each day*' and the call is out for '*school-lunch planners and public health officials*' to note these results.

These writings represent one interpretation of the implications of food reward for healthy eating. It basically claims that unless we severely limit rewards obtained from eating, we run the risk that the obesity epidemic will become even worse than it already is.

Eating food when hungry is obviously rewarding. This makes evolutionary sense. Since eating is necessary for survival, the signals needed to initiate the process of eating must be strong. But it does not follow logically that because initiating signals are strong, people will continue eating beyond satiation and sensory satisfaction. The argument rests on an assumption that the desire for reward is unlimited. This might indeed be the case in certain pathological states, but that it is generally the case is an assumption. In other rewarding human activities, it is well known that 'refractory periods' are necessary to fully enjoy the activity.

As noted above, people often consume substantially less of a food that provides more sensory pleasure than they do of a blander version of the food. That is, the more sensory rewarding a food is, the less people tend to eat of it. If this is the case, sensory satisfaction could promote healthier eating rather than the opposite. I will briefly discuss four sets of data suggesting that this might actually be the case.

The question can be phrased as whether 'quality' can replace 'quantity'.

The striatum is an area in the reward circuit in the brain, which has been implicated in many types of rewarding behaviours. Dopamine is an important neurotransmitter for the functioning of the striatum. Wang and coworkers [15] used positron emission tomography (PET) to measure the availability of dopamine receptors in the striatum in obese individuals and found an inverse relationship between BMI and availability of dopamine receptors. Since dopamine modulates reward circuits, this result suggests that dopamine deficiency in obese individuals may perpetuate pathological eating as a means to compensate for decreased activation of these circuits. That is, eating is driven by reward and continues until enough reward has been obtained. Under the assumption that well-tasting/high sensory quality foods provide more reward per energy unit than bland foods, this result supports the hypothesis that 'quality can replace quantity'.

In an experiment on the effects of trigeminal stimulation (hot spices) on hunger and satiety, HH Reisfelt and I came across a result which is relevant for the present discussion [16]. The subjects in the experiment attended the laboratory twice. On one of the visits, they were served an ordinary industrially manufactured tomato soup and were asked to report on hunger and satiety feelings, as well as on liking and wanting (and other measures which are not important in this context). During the other visit, they were served the same base soup, but this time, we had spiced the soup with chili.

We found that *satiety increased faster* when subjects ate the soup spiced with chili. Also, wanting of more of the spiced soup decreased faster over time than wanting of the base soup, even though wanting of the spiced soup was higher initially. The faster satiation and decrease in wanting when eating the spiced soup might conceal a wish to stop eating caused by a lower appreciation of the spiced soup than of the ordinary soup. We found, however, the opposite effect. The subjects liked better the spiced soup that satiated them faster. That is, eating a more rewarding food does not imply that normal subjects will eat more of it.

In a paper entitled 'eating what you like induces a stronger decrease in wanting to eat' [17], Lemmens et al. demonstrated just that effect with a randomized crossover design. In this experiment, the subjects came to the laboratory twice. During one visit, they were served a portion of chocolate mousse and during the other visit, a portion of cottage cheese. Caloric content was the same in both servings, and the subjects' hunger feelings were the same on the two visits. Chocolate mousse was liked more than the cottage cheese. By means of an image-based method, wanting for a large number of different foods was measured before and after intake of the foods. Lemmens et al. found that wanting dropped significantly for most food categories after intake of the chocolate mousse whereas this was not the case after eating the cottage cheese, which was liked less than the chocolate mousse. This result suggests that it is not a good idea to limit intake of liked foods in order to limit overall intake, under the assumption that people will tend to eat more of a food the more they want it.

Pelchat and coworkers [18] investigated brain activity using functional magnetic resonance imaging (fMRI) in people who had eaten two different diets for 1.5 days prior to the experiment. One group ate a monotonous diet, vanilla-flavoured Boost, whereas the other group ate a normal diet. The subjects in the normal diet group were also given two cans of Boost to familiarize themselves with it. Information about favorite foods was collected from all the subjects. After the 1.5 days of eating a normal diet or a monotonous diet, the subjects were scanned while they were told to imagine the sensory properties of a number of their favorite foods as well as of the Boost. The monotonous diet group showed greater activation to the craved or liked foods than to the monotonous Boost. Craving-related activations were detected in the hippocampus, insula and caudate. These areas have previously been reported to be involved in drug craving. Interestingly, no such differences were found for the normal diet group.

This result suggests that eating a monotonous diet induces stronger food cravings of liked foods that are often energy-dense. Under most circumstances, this will lead to a larger energy intake.

A better understanding of reward-related implications for healthy eating is, of course, not sufficient to fully understand and help prevent inappropriate eating behaviour. Habit and preference formation [19-21] and especially designing schemes where children (and other people) come to appreciate foods which are low in energy content is also important as is more research into self-regulation [22,23].

Before we understand these different basic scientific problems better, scientists should probably be a little less cocky in handing out advice to political decision makers.

Competing interests
The author declares that he has no competing interests.

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Flavour

SHORT REPORT Open Access

The important role of umami taste in oral and overall health

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Abstract

There is a close relationship between an individual's perception of umami taste and that individual's physical condition. Our newly developed umami taste sensitivity test revealed the loss of only the umami taste sensation with preservation of the other four basic taste sensations (sweet, salty, sour, and bitter) in some elderly patients. All such patients complained of appetite and weight loss, resulting in poor overall health. We also found that treatment of hyposalivation diminishes hypogeusia, indicating that salivation is essential to the maintenance of normal taste function. Based on these findings, we consider that improvement in salivary flow may serve as a treatment for patients with taste disorders. Umami taste stimulation increases the salivary flow rate because of the gustatory–salivary reflex. We used Japanese Kobucha (kelp tea: tea made of powdered tangle seaweed) to stimulate umami taste and promote reflexive salivation. Improvements were noted in salivation, taste function, appetite, weight, and overall health. Maintenance of umami taste function contributes not only to the preservation of good oral health but also to the general overall health in elderly people.

Keywords: Umami, Taste disorder, Dry mouth, Gustatory–salivary reflex, Overall health

Introduction

Enjoyment of taste should be one of the greatest pleasures in human life. However, aging is sometimes associated with decreased taste sensitivity. Loss of adequate gustatory function may induce a poor appetite, reduced dietary intake, and weight loss, particularly in the elderly [1]. In Japan, gustatory function is generally assessed using the filter paper disk test, in which a filter paper soaked with a taste-inducing chemical solution is placed on specific areas of the tongue and oral cavity. However, this test only assesses four of the five basic tastes: sweet, salty, sour, and bitter. Because the taste quality of umami, which is recognized as a fifth taste category [2-4], is not clinically assessed at present, information about umami taste disorders has yet to be accumulated. We recently reported the specific loss of the umami taste sensation with preservation of the other four taste sensations in some elderly patients [5,6]. The patients with loss of umami taste sensation also exhibited poor general health. In this article, we first review our studies, including that of our newly developed umami taste sensitivity test, and related studies concerning taste disorders with particular focus on umami taste disorders and overall health. Second, we examine the link between taste disorders and salivary flow because saliva assists and influences the detection of taste by allowing diffusion of the taste substances to the taste receptors, facilitating chemical interactions with food substances, and protecting the taste buds [7]. Finally, we discuss clinical application of taste stimulation as a remedy for dry mouth-related dysgeusia based on the gustatory–salivary reflex.

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Importance of umami taste sensation in the elderly

In our taste clinics, we sometimes meet elderly patients with taste disorders who complain of persistent impaired umami taste, although the other four basic taste sensations are normal. Because of the loss of umami taste, these patients experience appetite and weight loss, resulting in poor overall health. Unfortunately, the currently available clinical examinations result in a diagnosis of normal taste sensation in such patients with impaired umami taste because they have normal thresholds for the other four taste qualities. Umami taste receptors reportedly exist not only in the oral tissues but also in the gut. T1R receptors, which mediate umami taste, are expressed on cells of both the duodenum [8,9] and tongue, suggesting that the umami taste sensation functions in nutrient sensation and digestion in the gut [10]. This evidence indicates that the ability to detect umami flavors is very important for maintaining a healthy daily life. This is particularly true for the elderly because physiological functions and basic physical conditions decline with aging. Therefore, it is important that we are able to assess and treat umami taste impairment. At present, however, there is no clinical method with which to assess umami taste sensitivity.

Development of umami taste sensitivity test

We recently developed a filter paper disk method using monosodium glutamate (MSG) as a test solution to assess umami taste sensitivity [11] (Figure 1). We recruited 28 patients with taste disorders (45–78 years of age) and 184 controls without taste disorders (102 young subjects [18–25 years of age] and 82 elderly subjects [65–89 years of age]). Aqueous MSG solutions (1, 5, 10, 50, 100, and 200 mM) were prepared, and filter paper disks of 5-mm diameter were soaked in these individual solutions and placed on three specific oral sites innervated by different taste nerves. The lowest concentration that participants correctly identified was defined as the recognition threshold (RT) for umami taste sensitivity. We obtained five important results: (1) The RT of healthy controls differed at measurement sites that were innervated by different taste nerves; that is, the RT of the anterior tongue (AT) was higher than that of either the posterior tongue (PT) or the soft palate (SP) in both young and elderly individuals (Figure 2). (2) No significant difference in RTs was found between young adult and elderly individuals at any of the three different measurement sites, indicating that our method can be used to assess umami taste sensitivity regardless of the subject's age. (3) The RT of patients with taste disorders was higher before treatment than that of the healthy controls at all measurement sites. (4) The RT after treatment in these patients improved to the same level as that of the healthy controls. (5) The best cutoff RTs that showed the highest diagnostic accuracy (true positives + true negatives) were 200 mM MSG for the AT and 50 mM MSG for the PT and SP (Table 1). We concluded that our umami taste sensitivity test is useful for discriminating between normal and abnormal umami taste sensations because of the high diagnostic performance of this test (Table 1).

Clinical significance of umami taste perception

We assessed 44 patients who visited our clinic with a subjective feeling of dysgeusia using the new umami taste sensitivity test described above. We found that 16% of the patients showed a higher RT only for the umami taste; the RTs for the other four basic tastes were all within the normal range. All patients with an umami-specific taste disorder were >65 years of age, and all complained of appetite and weight loss with resultant poor overall health. Interestingly, the chief complaints of most of these patients were that food was not palatable and that they did not eat normally because of appetite loss [5]. Because all of these patients were elderly, one of the contributors to the development of umami taste dysfunction might be aging. Additionally, most of the patients with loss of umami taste also had systemic diseases (such as diabetes, gastric diseases, and/or depression) and/or oral diseases (such as oral stomatitis, oral candidiasis, and/or oral dryness) and were taking medications. Many of these diseases and medications are known to have side effects of taste disorders or hyposalivation, as described in the next section. After improvement of the patients'

Figure 1 Newly developed umami taste sensitivity test using filter paper disk test. Monosodium glutamate was used as an umami taste solution. Filter paper of 5-mm diameter was soaked with a taste-inducing chemical solution and placed on specific areas of the tongue and oral cavity using tweezers. The subjects were exposed to six different concentrations of umami solution: 1, 5, 10, 50, 100, and 200 mM. The lowest concentration at which the patient could detect and recognize the taste was defined as the recognition threshold.

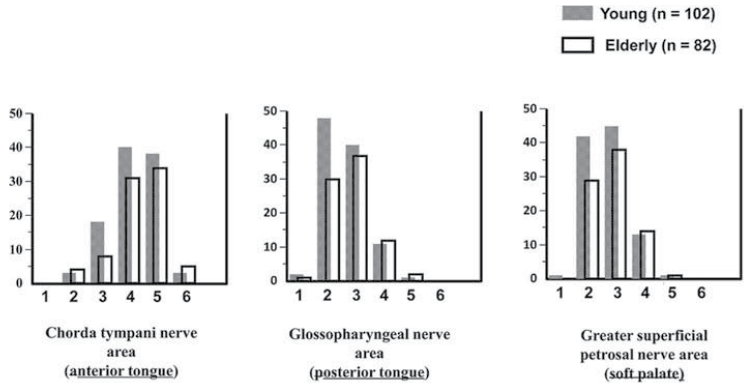

Figure 2 Distribution of umami taste sensitivity at the three different measurement sites. Umami taste sensitivity was examined at the three different measurement sites: the anterior tongue, posterior tongue, and soft palate. The subjects comprised 102 young and 82 elderly healthy participants. The x-axis shows the concentrations of the aqueous monosodium glutamate (MSG) solutions (1 = 1 mM, 2 = 5 mM, 3 = 10 mM, 4 = 50 mM, 5 = 100 mM, and 6 = 200 mM). The y-axis indicates the number of participants who correctly recognized the presence of MSG at each concentration of MSG.

umami taste sensitivity, the patients also experienced remarkable improvements in their appetite and weight because food regained its palatability. All were pleased with the improvement in their health [6,11]. These results indicate that the umami taste sensation is very important to the maintenance of good health in the elderly.

Link between taste disorders and salivary flow

Physiological evidence supports the strong effects of saliva on taste perception [12]. Taste substances should be dissolved within the salivary fluid layer to reach and stimulate the taste receptors during the initial process of taste perception. Additionally, many drugs prescribed for elderly people reduce salivary flow as a side effect. Such drugs include remedies for stomach and bowel disorders, antihypertensives, muscarinic blockers, antihistamines, and antidepressants [13-16]. We examined the relationship between the salivary flow rate and taste threshold to identify how hyposalivation influences hypogeusia in the elderly. Our study demonstrated that the stimulated salivary flow (SF) measured with the gum test [17] was significantly lower in subjects with taste disorders than in normal subjects (normal SF > 10 ml per 10 min) (Figure 3). These findings suggest that hyposalivation is closely associated with taste disorders. Moreover, our recent study on xerostomia (subjective feeling of dry mouth) using parameters of the minor salivary gland flow (MF) and SF showed that (1) the MF and SF were both significantly lower in subjects with dry mouth than in controls, (2) there was a positive correlation between MF and SF in controls but not in subjects with dry mouth, and (3) there was a significantly larger reduction in MF than in SF in subjects with dry mouth but not in controls. These results indicate that dry mouth is more closely related to a reduction in MF than in SF [18]. MF might be closely associated with taste disorders because the minor salivary glands are widely distributed throughout the oral mucosa, including the taste buds, and maintain a healthy condition in the presence of elements such as lysozyme, peroxidase, and histatin.

Table 1 Diagnostic performance of umami taste sensitivity test for assessment of umami taste disorder

	AT	PT	SP
AUC	0.95	0.97	0.97
Cut-off value	200 mM MSG	50 mM MSG	50 mM MSG
Sensitivity	0.86	1.00	1.00
Specificity	0.94	0.83	0.82
PPV	0.83	0.67	0.65
NPV	0.95	1.00	1.00
Diagnostic accuracy (TP + TN)	0.92	0.87	0.86

AT anterior tongue, *PT* posterior tongue, *SP* soft palate, *AUC* area under the receiver operating characteristics curve, *PPV* positive predictive value, *NPV* negative predictive value; Diagnostic accuracy = true positives (TP) + true negatives (TN).

Remedy for dry mouth-related hypogeusia based on the gustatory-salivary reflex

The umami taste is known to induce the gustatory–salivary reflex [19,20]. We recently examined the labial MF response to the five tastes in 11 healthy male subjects (mean age, 31 years) and found that the order of relative MF responses from highest to lowest was MSG (umami) > citric acid (sour) > NaCl (salt) = sucrose (sweet) = quinine (bitter) [21]. Furthermore, the increase in salivation in response to the umami taste was long-lasting, whereas the increase elicited by sour stimulation diminished immediately

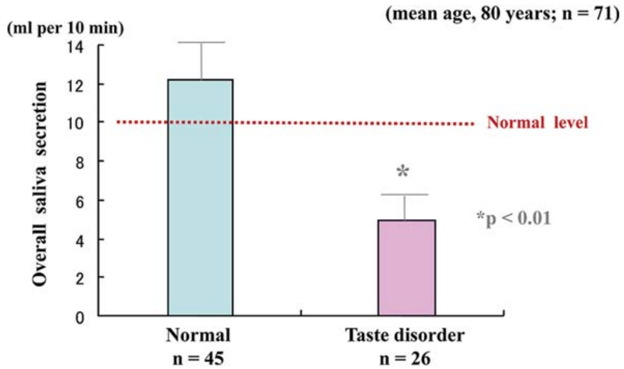

Figure 3 Relationship between overall saliva secretion and taste sensitivity in the elderly. Overall saliva secretion in subjects with a taste disorder was significantly lower than that in subjects with normal taste sensation ($p < 0.01$). Overall saliva secretion was measured using the gum test (normal level > 10 ml per 10 min).

(Figure 4). This longer lasting effect of MSG on the reflexive minor salivary gland secretion was similar to the changes observed in the overall salivary secretion (total secretion from the three major salivary glands and the minor salivary glands) [22]. We propose the use of Japanese Kobucha (kelp tea: tea made of powdered tangle seaweed), which is rich in MSG, as a remedy for dry mouth-related hypogeusia. We speculate that the umami substance in our study strongly enhanced the secretion of saliva from the minor salivary glands. This saliva contains abundant mucin, which lubricates the mouth [23] and maintains a healthy condition of the taste buds. Our clinical data showed that most patients with dry mouth-related hypogeusia were relieved of their symptoms. Thus, umami taste stimulation could be an effective therapy free of side effects in patients with dry mouth and dry mouth-related hypogeusia.

Conclusion

Taste dysfunction has a negative effect on health. In particular, loss of umami taste causes deterioration in overall health because of appetite and weight loss. Taste function and salivation are closely related to each other. The sense of umami taste promotes salivary secretion, and saliva strongly influences oral functions such as taste sensation. Thus, umami taste function seems to play an important role in the maintenance of oral and overall health.

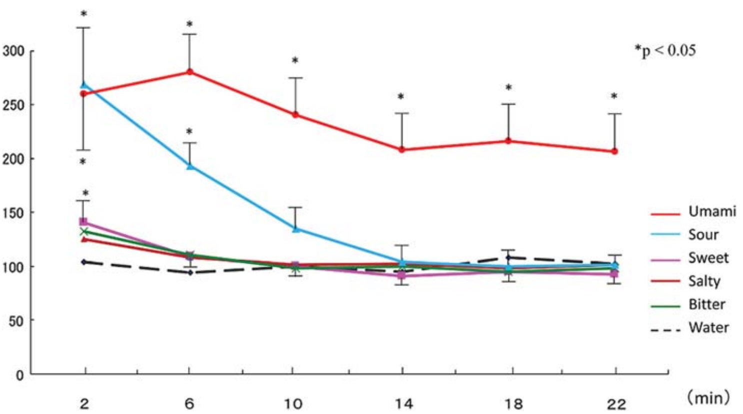

Figure 4 Labial minor salivary gland flow responses to the five tastes. Minor salivary gland flow responses from highest to lowest were monosodium glutamate (umami) > citric acid (sour) > NaCl (salt) = sucrose (sweet) = quinine (bitter). The salivary secretion was expressed as a percentage of the control.

Ethics statement

The present study was conducted according to the guidelines in the Declaration of Helsinki (http://www.wma.net) and was approved by a local ethics committee (the Ethics Committee of Tohoku University Graduate School of Dentistry, approved Nos. 22–21 and 23–23). Written informed consent was obtained from all participants.

Abbreviations

MSG: monosodium glutamate; RT: recognition threshold; AT: anterior tongue; PT: posterior tongue; SP: soft palate; SF: stimulated salivary flow; MF: minor salivary gland flow.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

NS, SSK, and TS contributed equally to the manuscript and approved the final version of the manuscript. All authors read and approved the final manuscript.

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Taste receptors in the gastrointestinal system

Ana M San Gabriel

Abstract

In the last 15 years, advancements in molecular biology have unraveled the proteins that function as taste receptors. There are at least five taste qualities that are consciously perceived, sweet, sour, salty, bitter, and umami. Of these five, sour and salty are mediated by ion channels, whereas the perception of sweet, umami, and bitter tastes is mediated by G protein-coupled receptors (GPCRs). These taste GPCRs belong to the TAS1R and TAS2R gene families. There are other nutrient-binding GPCRs whose taste function is still being studied such as CaSR, GPRC6A, GPR92, or GPR120. It has been suspected for more than a century that the gut can sense the chemical composition of foods. The description of multiple taste GPCRs in gastrointestinal (GI) cells suggests that there are nutrient-sensing mechanisms in the GI tract, oral, gastric, and intestinal mucosa. Oral sensing seems to mainly influence food discrimination and nutrient appetite, while post-oral chemosensors may relate to nutrient utilization and inhibition of appetite. The most common accepted view is that taste GPCRs are present in enteroendocrine cells among others also known as chemosensory cells. These cells express taste receptors and other taste-related genes. Although, functional cells of the GI mucosa that are not enteroendocrine or brush cells such as enterocytes or gastric cells may also hold receptive mechanisms that transduce the presence of certain nutrients in ingested foods and regulate gastric functions. This paper examines the importance of food chemical signals in their association with the neuroendocrine mechanisms they trigger, which are the core for metabolism and appetite regulation.

Keywords: Chemical sensing, Gut, Taste receptors, Vagus nerve, Peptide hormones, Umami, GPCRs, Cephalic phase

Introduction

Sugars, organic acids, minerals, alkaloids, or amino acids in foods bind to their corresponding taste receptors acting themselves as chemical messengers and inducing one of the known five taste qualities, sweet, sour, salty, bitter, and umami or savory taste, the taste of glutamate [1]. This interaction between single nutrients and taste receptors serves three basic purposes, to identify and discriminate foods and drinks, to promote or discourage ingestion, and to facilitate nutrient utilization by learned anticipatory or cephalic phase responses [2]. In his latest review, Alexander Bachmanov et al. describe taste receptors 'as one of the interfaces between internal and external milieus' [1]. Indeed, taste receptors appear to inform the brain of the chemical composition of foods and in turn, the brain responds accordingly with learned anticipatory responses to maintain body homeostasis prior to nutrient absorption [3]. Anticipatory responses that involved brain reflexes after sensory stimulation reduce the impact of food in our body. If taste receptors in the oral cavity are part of the conscious perception of the chemical composition of foods, it is not surprising that the same taste receptors from the oral cavity are also found in the gastrointestinal tract (GI). There, taste receptors also sense the chemical milieu of the luminal contents. But in the gut, the function of taste receptors is not to identify foods, rather to transduce the nutrient signal into neuropeptide hormones, vagus nerve activation, and nutrient utilization, all important modulators of digestive processes, appetite, and metabolism [4,5].

Taste, flavor, and gut chemical sensing

Newborn infants have a strong innate liking for sweet and umami tastes while manifesting aversion for bitterness [5]. These inborn responses may predispose the infants for the acceptance of sweet and umami taste compounds present in breast milk [6,7]. It is not until they experience the volatile components of the flavor that infants learn to prefer or reject certain foods [8]. This learning process for flavor preference consists on classic Pavlovian conditioning reflexes from the post-oral nutritional effects of foods [3,9]. Flavor allows us to learn

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the association between foods and their metabolic and physiological outcome. This is especially important in human adults because we consumed a varied diet. By learning the relationship between the sensorial attributes of foods and their post-oral outcome, the brain can predict the physiological and metabolic impact that specific meals may have in our body [9]. The cephalic phase insulin release (CPIR) after glucose ingestion or the induction of salivary, gastric, and pancreatic secretions in response to a meal are good examples of conditioned physiological responses [3]. In fact, oral ingestion of glucose generates higher insulin release than a similar amount of glucose directly injected intravenously [10,11]. The higher insulin secretion after glucose ingestion most likely results from the strengthening of CPIR with the stimulation of sweet receptors in gut enteroendocrine cells that further enhance blood insulin via incretin hormones such as glucagon-like peptide 1 (GLP-1). The effect of glucose binding to sweet receptors in the gut goes as far as to increase the number of glucose transporters in enterocytes [12]. This oral and post-oral stimulation by glucose illustrates clearly that intestinal signals reinforce taste information allowing for more efficient physiological responses to meals in accordance to their chemical composition.

Overview of taste receptors

In the last decade, taste physiologists, geneticists, and molecular biologists have discovered that receptors for sweet, umami, and bitter tastes are members of the G protein-coupled receptor (GPCR) proteins [1]. Sweet and umami receptors belong to the T1R family, whereas bitter receptors are part of the T2R family [13,14]. The family of T1Rs is included in the class C group of protein (metabotropic glutamate/pheromone) receptors with three proteins, T1R1, T1R2, and T1R3. In humans, the combination of T1R2 with T1R3 functions as a sweet receptor. Many varied compounds taste sweet to humans, from sugar alcohols and glycosides to amino acids and proteins [1,15,16]. Receptors for umami result from the combination of T1R1 and T1R3, T1R3 being common for sweet and umami taste [1,13,16]. Compounds with a strong umami taste to humans comprise L-amino acids, such as glutamate and aspartate, and 5′-ribonucleotides [15]. Other substances with weaker umami attributes are theogallin, theanine, ibotenic, tricholomic, succinic, and gallic acids besides several peptides [1]. There is also evidence for considering as umami receptors splicing variants of metabotropic glutamate receptors types 1 and 4 (mGluR4 and mGluR1), which belong to the same family of T1Rs, and the N-methyl-D-aspartate (NMDA) glutamate ion channel receptor [1,17,18]. The perception of bitter taste that arouses innate aversive behavior includes a large variety of compounds, mostly toxic chemicals from plants or microorganisms. Bitter taste receptors belong to the T2Rs (taste receptor type 2) of the class A of GPCR family (rhodopsin like). Humans exhibit 25 TAS2R bitter-receptor genes among which 20 receptors have been already de-orphanized by using heterologous *in vitro* cell systems [19]. Some of these receptors are specific to a single or a few bitter compounds, whereas others are tuned to a wide variety of chemical compounds. For salty taste, after many years of conjecture, the epithelial sodium channel (ENaC) was proved to be responsible for the transduction of salty taste, considering sodium chloride and lithium chloride the exemplary salty compounds [20]. Because ENaC functions as a sodium transepithelial transporter in many tissues such as the kidney or the lungs, this ion channel is expressed in many epithelial tissues. Thus, its simple existence in the GI does not help to consider the taste-like function of sodium salts throughout the alimentary canal and this is the reason for there being no studies on salt sensing in the GI. About sour taste, although a number of contenders have been suggested as sour taste receptors, they are still being disputed [1,19]. Finally, there are other GPCR nutrient receptors that, although have been described in the taste tissue, their taste-specific qualities are still under investigation. They are receptors that can bind to a wide variety of amino acids such as the extracellular calcium-sensing receptor (CaSR), which has been linked to kokumi substances, calcium, and large aromatic amino acids, the GPCR family C subtype 6A (GPCR6A) that binds to basic amino acids, or the G protein-coupled protein 92 (GPR92) that binds to peptone and may be also involved in the perception of umami taste [4,21-23]. Interestingly, in GI cells, these receptors have been associated with the regulation of gastric secretion, control of satiation, and GI motility [4,24]. There are other nutrient receptors that have been described in oral and post-oral tissues such as the G protein-coupled receptor 120 (GPR120) and the free fatty acid receptors 1, 2, and 3 (FFAR1, FFAR2, FFAR3). GPR120 and FFARs bind to free fatty acids of different lengths. GPR120 and FFAR1 (a.k.a., GPR 40) have been considered candidates for the oro-sensory perception of fats [25].

The significance of gut sensing via taste receptors

Chemical sensing in the gut was first proposed in the 19th century by the Nobel price physiologist Ivan Pavlov through his *nerve antenna theory* in which he assumed that nerve endings were exposed to the chemical milieu of the luminal content [11,26]. Later on, Bayliss and Starling in 1902 observed that by applying protons at the duodenum, there was a robust secretion of pancreatic secretions and the response was not mediated by nerves but rather by a secreted compound [27]. This compound was named 'secretin' and later designated as a *hormone*. As such, secretin is an emissary that carries chemical information to the predetermined target through the blood. With time, it became clear that intestinal nerves did not project to the surface of the intestine, and the *intestinal sensor cell* theory arose in the 1970s due to Fujita and Kobayashi [28]. They suggested the presence of bipolar nutrient-sensing cells. These cells can interact with nutrients at the lumen thanks to having projections toward the surface of the stomach and intestine [29]. The view that is most accepted today considers that taste GPCRs are present in 'open' enteroendocrine and brush cells also known as chemosensory cells. The enteroendocrine cells are the ones that dispatch nutrient information via peptide hormones and bioactive amines to the corresponding organs either via endocrine or vagal pathways as shown in Figure 1 [11,26]. The binding of single amino acids such as L-glutamate, L-phenylalanine, L-tryptophan, L-arginine, or L-lysine to their corresponding GPCRs (T1Rs, mGluR1, CaSR, or GPRC6A) in the stomach regulates the secretion of gastric hormones such as serotonin, gastrin, somatostatin, and ghrelin, the only known hormone that enhances hunger [4,30,31]. In rats and dogs, glutamate in the stomach activates the nerve endings of the vagus nerve via serotonin and nitric oxide, which in turn enhances gastric secretion also through vagus nerve responses [32,33]. Vagal efferent fibers, the ones carrying information from the brain, release acetylcholine upon stimulation. This vagal neurotransmitter is a potent activator of the proton pump of parietal cells, the cells in charge of producing hydrochloric acid that is under the regulation of gastrin and somatostatin [24,34]. In the duodenum, long-chain fatty acids, peptides, amino acids, and bitter compounds can induce the release of cholecystokinin (CCK) from I cells. Glucagon-like peptide 1 (GLP-1) is secreted from L cells in the ileum with sugars, long-chain fatty acids, amino acids, and also bitter compounds; whereas the di-peptide tyrosine-tyrosine (PYY) comes from the colon as a result of short-chain fatty acids [4]. These regulatory GI hormones can signal nutrient information to the brain because the projections of the vagus nerve that lie underneath the lining of the GI contain receptors for serotonin, CCK, GLP-1, and PYY (Figure 1) [11]. In the brain, centers such as the arcuate nucleolus of the hypothalamus or the limbic system integrate nutrient information to regulate food intake, body metabolism, and the reward system.

Conclusion and perspectives

With the mounting body of evidence for the function of nutrient receptors in oral, gastric, and intestinal lining as mediators of food signals, it is becoming clearer that food components hold information that goes beyond their caloric values. Single sugars, amino acids, or even free fatty acids are not only a fast source of energy because they do not require digestion but also they provide strong signals from receptors in the mouth and the stomach before digestion with pancreatic juices. Foods that

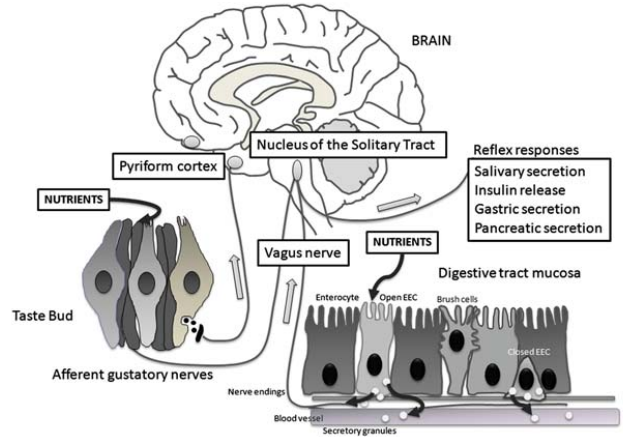

Figure 1 Schematic representation of the taste and gastrointestinal (GI) input. Schematic representation of the taste and gastrointestinal (GI) input to the brain from the gustatory and vagus nerves, respectively. The gustatory system is represented by taste cells in onion-like taste buds and their gustatory nerves. Corresponding to the GI system, there are two enteroendocrine cells (EEC), one that is open to the lumen-releasing cholecystokinin (CCK) and glucagon-like peptide 1 (GLP-1) in response to luminal nutrients and one that is closed. Vagal fibers are located underneath the GI mucosa in close contact with hormone secretions. The signals from the gustatory system reach the rostral nucleus of the solitary tract whereas visceral impulses terminate at the caudal nucleus of the solitary tract. From the nucleus of the solitary tract, gustatory and visceral information projects to several brain regions including the amygdala, the hypothalamus, and the ventral posterior nucleus of the thalamus. These regions are involved with ingestive motivation, physiological reflexes, and energy homeostasis.

are rich in free nutrients, such as either soup stocks or cured and fermented or aged meats and cheeses, offer clear gustatory and odorant cues. Having sharp taste and odorant sensorial experiences allows for more robust information to the brain, stronger learned anticipatory responses, and a better handling of nutrients in the body. This could be a key factor for a more efficient food intake regulation, which is a key to avoid overeating and overweight. More research is necessary for a better understanding of the integration of taste and visceral signals. This line of research may help better weight management in overweight adults and other metabolic diseases related to nutrient homeostasis in the body.

Abbreviations

CaSR: calcium-sensing receptor; *CCK*: cholecystokinin; *CPIR*: cephalic phase insulin release; *ENaC*: epithelial sodium channel; *FFARs*: Free fatty acid receptors; *GI*: gastrointestinal; *GLP-1*: glucagon-like peptide 1; *GPCR6A*: GPCR family C subtype 6A; *GPR92*: G protein-coupled protein 92; *GPR40*: G protein-coupled receptor 40; *GPR120*: G protein-coupled receptor 120; *mGluR*: metabotropic glutamate receptor.

Competing interests

The author declares that she has no competing interests.

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Flavour

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Neuroenology: how the brain creates the taste of wine

Gordon M Shepherd

Abstract

Flavour science is concerned with the sensory appreciation of food. However, flavor is not in the food; it is created by the brain, through multiple sensory, motor, and central behavioral systems. We call this new multidisciplinary field "neurogastronomy." It is proving useful in integrating research findings in the brain with the biomechanics of generating food volatiles and their transport through retronasal smell. Recent findings in laboratory animals and in humans give new insights into the adaptations that have occurred during evolution that give humans an enhanced flavor perception. This process will be illustrated by an analysis of how the brain creates the taste of wine. The successive stages of the biomechanics of movement of the ingested wine and transport of the released volatiles will be correlated with activation of the multiple brain mechanisms, apparently engaging more of the brain than any other human behavior. These stages include the initial cephalic phase, visual analysis, ingestion, formation of the wine perceptual image, formation of the wine perceptual object, swallowing, and post-ingestive effects. This combined biomechanic and brain mechanism approach suggests a new discipline of "neuroenology (neuro-oenology)," adding to the contributions that science can make to the enhanced quality and appreciation of wine.

Keywords: Wine, Retronasal smell, Wine image, Wine perceptual object, Fluid mechanics

Interest in food flavors is expanding rapidly, driven by a widening interest in food and concerns about the rising incidence of obesity and diseases related to unhealthy eating. While most interest is focused on the food, its composition, and the perceptions that it brings forth (see other contributions to this symposium), this has left large gaps of knowledge about the specific brain systems that create the perceptions. This approach to flavor through brain mechanisms has been termed neurogastronomy [1]. Here we outline some of the principles that are the basis for this new approach and then use wine tasting as an example.

Some principles of neurogastronomy

To begin, *flavor is not in the food; it is created from the food by the brain* [2]. There is a clear analogy with other sensory systems. In vision, for example, color is not in the wave lengths of light; color is created from the wave lengths by the neural processing circuits in the visual pathway; these include center-surround interactions for color-opponent mechanisms [3]. Similarly, pain is not in the agents that give rise to it, such as a pin or a toxin; pain is created by the neural processing mechanisms and circuits in the pain pathway, together with central circuits for emotion [4].

Improved understanding of these mechanisms should give ultimate insight into the "qualia" of sensory perception. Flavour is an attractive system for contributing to these insights.

Second, *flavor is a multi-modal sensation*. It is *multi-sensory*, involving *all the sensory systems* of the head and upper body [5]. This is nicely demonstrated in a quote [1] attributed to the famous chef Paul Bocuse:

> The ideal wine … satisfies perfectly all five senses: vision by its color; smell by its bouquet; touch by its freshness; taste by its flavor; and hearing by its "glou-glou".

At the same time, flavor is *multimotor*, involving *all the relevant motor systems*. These include the obvious muscle systems of the tongue, jaw, and cheeks, critical

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for manipulating the food and drink in the mouth [6]. Recent research suggests that the movements of the tongue in manipulating food in the mouth are more complex than the movements used in creating the sounds of speech [7]. The motor systems also include those of the neck involved in swallowing, plus those in each sensory system (inner ear, eye muscles), plus the diaphragm and chest and pelvic muscles involved in breathing. They also include the glands for producing saliva for solubilizing and initiating digestion the food in the mouth. *Flavor is therefore special in being always an active sense*, with motor systems essential to activating the sensory pathways and central brain systems.

Third, *much of flavor is due to retronasal smell*, that is, smell that occurs when we are *breathing out*, to carry the volatiles from the mouth to the nasal cavity. This can truly be called our unknown sense. It was early recognized [8] that smell is a dual sense, reflecting the fact that odor stimuli can be delivered by both orthonasal (sniffing in) and retronasal (breathing out) routes. Most of what we know about smell, both in humans and laboratory animals, comes from studies of orthonasal smell. Research on retronasal smell is relatively recent [9-11].

There is evidence going back to Victor Negus [12] that most mammals have a relatively long palate and nasopharynx for retronasal smell, in contrast to humans who have a relatively short palate that places the back of the mouth, where volatiles from the mouth are produced, relatively close to the nasal cavity for sensing by smell. Humans therefore appear to be adapted for retronasal smell and flavor.

Fourth, we are normally entirely *unconscious of the retronasal contribution to flavor*. The touch of the food in the mouth and the conscious sensations of the basic tastes emanating from the tongue "capture" our awareness of the food and refer all other sensations, including retronasal smell, to the mouth [2]. Flavor therefore has the quality of an *illusion*. This makes flavor vulnerable to many influences, as is well recognized by food producers in formulating and promoting their foods. Food producers spend millions on research to use the sensory illusions to influence our choices of food, in our homes as well as in the supermarket and the school cafeteria [13]. We therefore need a better understanding of retronasal smell in order to develop public policies based on better understanding of brain mechanisms that can lead to eating healthier food.

Fifth, as already indicated, we must keep in mind the underlying principle that "Nothing in biology makes sense except in the light of evolution" [14]. This is essential in understanding how flavor perception and its associated sensory, motor, and central behavioral systems have been built into humans over the past million years and are the basis for current eating habits. Wrangham has hypothesized that the control of fire by early humans enabled them to invent cooking, which increased the energy in food, thus enabling the larger brains of Homo sapiens [15]. Cooking would obviously have also enhanced the flavors of the food. From this perspective, retronasal smell and flavor may thus have played a central role in how we became human. The adaptations of the human head for playing this role have been discussed in detail by Lieberman [7].

A new vision for flavor science

It is obvious from the range of these principles that brain mechanisms in flavor perception have far reaching ramifications in modern society. It has been argued that this requires a much enlarged framework for understanding flavor. As discussed in a recent conference [16], this new all-embracing vision for a science of food and its flavors begins with the principle cited that biology makes sense only in the light of evolution. A corollary for the neuroscientist is "Nothing in the brain makes sense except in the light of behavior". The multiple neural mechanisms involved in producing flavor include sensory, motor, cognitive, emotional, language, pre- and post-ingestive, hormonal, and metabolic. It can be claimed that more brain systems are engaged in producing flavor perceptions than in any other human behavior. These mechanisms are in play from conception through old age. Understanding them requires research on both humans and laboratory animals. In addition to insights into normal function, this research is needed for dealing with clinical disorders, ranging from obesity to Parkinson's, and including dental medicine. Food producers carry out their own research on the brain mechanisms to draw consumers to products with attractive flavors but in too many cases with unhealthy consequences; the public needs to be as well informed about the brain mechanisms so that together more healthy foods can be produced and consumed. Food activists play roles in pressing for sustainable diets, anti-poverty policies, responsible agriculture; and preventing the consequences of climate change. Finally, new initiatives in flavor research are urgently needed with funding for broad attacks that will benefit nutrition and public health.

Mechanisms for flavor images and flavor biomechanics

In order to understand the multisensory integration that underlies flavor perception, we need to begin with how the brain represents the sensory world. Most sensory systems use neural space to represent their stimuli. This is most obvious in the somatosensory system, where the body surface is represented across a strip of cortex as a "homunculus". It is also obvious in vision, where the external visual field is represented by the visual field in the primary visual cortex. Less obvious is the auditory system.

How is sound frequency, which has no spatial property, represented in the brain? Research has shown that frequency is represented by a frequency map laid out across primary auditory cortex. The map is a simple progression of frequency for the cat, but a much more elaborate progression for the bat which has an enlarged area for the frequency it uses for locating prey [17].

Olfactory stimuli, in the form of different molecules, also have no spatial property. What are the neural mechanisms by which the information carried in an odor molecule is represented in the brain? In rodents, it was early established that stimulation with a given type of odor molecule elicits a pattern of activity in the glomerular layer of the olfactory bulb [18]. We called these "odor maps"; they are also called odor images or "smell images". A critical finding was that although the patterns for different odors are extensive and overlapping, they are different for different molecules [19], even if they differ by only a single carbon atom and its two hydrogens [20]. Further behavioral experiments have shown that rodents can easily distinguish these fine differences [21], a sensitivity far greater than that for antibody-antigen recognition in the immune system.

Breakthrough experiments identified the odor receptor molecules [22] and showed that subsets of receptor cells expressing the same receptor gene project to differing sites in the glomerular layer, thus supporting the concept that space plays a role in encoding odor molecules. We are constructing computational models in three dimensions to gain further insight into how these images are formed within the olfactory bulb [23]. Further processing transforms the odor images in the olfactory bulb, representing the information in the odor molecules, to "odor objects" in the olfactory cortex, which are in a form that can be integrated by the brain into odor perception [24].

These results have been revealed by experiments using orthonasal smell. This scheme is believed in general to apply to the neural processing mechanisms in retronasal smell. However, the dramatic difference is that when retronasal smell is activated by volatiles released from the back of the mouth during exhalation, all the associated systems involved in flavor perception are also activated. The question then arises: How is this array of systems coordinated? The mechanisms of activation are presently little understood, beyond what has already been mentioned about the complex movements of the tongue and the equally complex mechanisms of swallowing, coordinated with respiration.

Activation of the multimodal systems of flavor can be seen to be tightly linked to the movement of the food and drink through the mouth together with the movements of muscles and air during respiration. We can call these motor events the *biomechanics of flavor*. The biomechanics of the movement of air past the back of the mouth involves more specifically a subset of engineering problems that fall under the category of *dynamic fluid mechanics*. This approach has revealed complex flow patterns of air through the nasal cavity during orthonasal [25-27] smell. The challenge now is to do the same for the flow patterns of air through the oro- and nasopharynx during retronasal smell.

Neuroenology (neuro-oenology): from biomechanics to the taste of wine

Building on the principles discussed above, let us use wine tasting as a specific example.

Hundreds of books have been written about wine tasting [28,29]. Most focus on the grapes, the vintages, and the techniques of tasting. Most include comments on the roles that the different senses play but few on recent studies of their pathways and mechanisms in the brain.

Here we wish to contribute to building a science of wine tasting by approaching the wine from the perspective of the brain. For this, we need to unite the biomechanics of movement of wine through the mouth and the movement of air through the oro- and nasopharynx into the nasal cavity, with the activation of, and control by, the multimodal brain systems. Recently, at a symposium on wine, I drew together these aspects to use wine tasting as an example of neurogastronomy and will use it here to suggest some principles that may be called neuroenology (or neuro-oenology in British spelling).

We start with the key role proposed for retronasal smell. What is the proof that the retronasal pathway is open during tasting of the wine? Fluoroscopic observation has been made of the head and neck during ingestion of liquid; an example is available on YouTube (https://www.youtube.com/watch?v=umnnA50IDIY29). As can be seen, the nasopharynx is clearly open with the fluid in the mouth and closes when swallowing. This can be easily confirmed by personal experience; with wine in the mouth, breathing in and out occurs while sensing of the taste of the wine occurs, which is shut off when swallowing.

We are currently carrying out a quantitative analysis of this process, involving the biomechanics of wine in the mouth and fluid dynamics of the volatiles in the airway, which is still at an early stage. However, at this point, it is possible to suggest the main steps at the core of the wine tasting experience.

An animation was shown at the meeting to illustrate these events. Table 1 summarizes the most important steps.

The first step (*cephalic phase*) occurs entirely in the head, consisting of the accumulated experience of the taster with wine in general and anticipation of this wine or wine tasting in particular. The expected flavor of the wine is thus due entirely to vision and to the imagination. The wine is then poured and *preliminary analysis* carried out of it in the glass. Closer visual inspection strongly influences the expected flavor ("We eat first with our eyes" [30]). The aroma (bouquet) is the first encounter

Table 1 Brain and biomechanics stages in wine tasting

Brain systems	Biomechanics
Cephalic phase (vision)	
Preliminary analysis (vision)	Orthonasal smell
Ingestion	Tongue, exhalation, retronasal smell
Initial analysis	Tongue, exhalation, retronasal smell
Forming the wine perceptual image	Tongue, exhalation, retronasal smell
Forming the wine flavor object	Tongue, exhalation, retronasal smell
Swallowing	Automatic motor action
Post-swallowing	Exhalation, retronasal smell

with the olfactory sense, due to orthonasal smell acting together with vision.

With *ingestion*, the wine is placed carefully in the mouth for maximum exposure to the senses. *Initial analysis* occurs by each of the major internal senses: touch and mouth-feel, taste, retronasal smell, and hearing. Touch is critical in locating the wine in the mouth; as with food, it fools the brain into assuming that all the "taste" of the wine comes from the mouth. The motor systems for saliva and muscle movement of the tongue, cheek, and jaw are activated. Thus, like food, wine taste is also an active perception. Each sense initially forms its own *sensory image*.

Simultaneous activation of the multiple sensory systems spreads from the primary to the surrounding association areas. Their common action begins to form what can be called the *wine perceptual image*. This combined image is *conscious*, except that it contains the illusion that its olfactory part is coming from the mouth and is part of "taste". Experienced tasters enhance the taste by breathing in through the lips to aerate the wine in the mouth, although the effect does not reach the nose until breathing out through the nasopharynx. The taste is also enhanced by expert movements of the tongue to move the wine completely over all the taste buds of the tongue and pharynx. As mentioned, these movements are more complex than the tongue movements in forming speech. The movements also mix the wine with the saliva. Working against these mechanisms for enhancement is sensory adaptation, which occurs at all levels of the sensory pathways, from the receptors and their second messenger systems to the successive synaptic relays on the way to the cortex.

As processing in the sensory pathways continues, the images which were formed to represent the external sensory stimuli are transformed into central representations of the entire *flavor object*, i.e., in this case, the *wine flavor object*. That is, *the images in the languages of the senses are transformed into objects in the language of the brain*. In addition to the sensory pathways for discrimination, central behavioral systems are engaged, also in the language of the brain. Memory systems mediate recognition. Emotion systems mediate feelings. Dopamine systems mediate reward. Motivation systems calculate continuance of drinking. And most important for humans, language systems enable categorization that can be formulated by ourselves and communicated to others. Retronasal smell continues to flood the olfactory receptors with volatiles from the wine in the mouth. This maximum activation of flavor systems is depicted in Figure 1.

Figure 1 Analyzing the wine flavor object. Summary of activation of flavor systems related to wine tasting. Sensory pathways include touch, taste, olfaction, visual cortex (audition not shown). Motor pathways include mouth: tongue, cheek, jaw, glands producing saliva; pharynx; lungs for inhalation and exhalation. Ellipses represent activation of central brain systems for memory, emotion, motivation, reward, and language. Adapted from [31].

For many people, this represents the peak of the wine tasting experience. However, there is one more step. The prefrontal cortex decides when all the systems have reached their culmination, and the conscious decision is made to terminate by *swallowing*. The soft palate closes to prevent aspirating wine into the nasopharynx, the epiglottis closes to prevent it entering the trachea, and the complex systems of muscles of the tongue, pharynx, neck, and lung carry out swallowing automatically. It is one of the most complex behaviors in mammalian life.

But the sensory stimulation of the wine tasting is not yet over. In the post-swallowing phase, the wine coating the pharynx still is carried to the smell receptors in the nose by retronasal smell, providing the "longueur on bouche" ("length in the mouth"). Together with the lingering activity in the systems for memory, emotion, and motivation, it contributes to the final conscious evaluation of the wine. In addition, the *post-ingestive* period is characterized by metabolic effects of the wine in the gut [32]. In the case of studies of this period during food consumption, there is increasing interest in these actions on isolated taste buds and on the metabolic effects of carbohydrates that contribute to obesity. In the case of wine, the alcohol content has actions on central systems for craving leading to inebriation [33], reminding us that, as with so many things in life that give us pleasure, in excess, wine is also a potential drug of abuse.

In summary, the stages in wine tasting have traditionally been characterized by the tasters. Increasing knowledge of brain mechanisms and the associated biomechanics of the wine in the mouth and the volatiles in the airway gives a new enlarged framework for a deeper understanding of this most complex experience of flavor among all of human foods.

Competing interests
The author declares that he has no competing interests.

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Flavour

REVIEW Open Access

The pleasure of food: underlying brain mechanisms of eating and other pleasures

Morten L Kringelbach[1,2]

Abstract

As all chefs know, great food can have a transformational impact. A great deal of recent research has gone into using the new techniques from molecular gastronomy and gastrophysics to create innovative meals with delicious original textures and flavours. These novel creations have elicited much excitement from food critiques and diners alike. Much stands to be gained if these developments were to be matched by a better understanding of how the pleasure of food comes about in the brain. This review summarises the current state-of-the-art of the science of pleasure and specifically the brain's fundamental computational principles for eating and the pleasures evoked. It is shown how the study of food has advanced our understanding of the unitary pleasure system that is used for all pleasures. As such, these novel insights may come to serve as a guide for chefs of how to combine science and art in order to maximise pleasure—and perhaps even increase happiness.

Keywords: Dinner, Gastronomy, Brain, Pleasure cycle, Satiety, Satiation, Hedonic, Pleasure, Food, Multimodal integration, Insula, Operculum, Orbitofrontal cortex, Cingulate cortex, Wanting, Liking, Learning, Anhedonia

Introduction

The novella "Babette's Feast" by the Danish writer Karen Blixen (writing under her nom du plume of Isak Dinesen) is set in the 1870s, describing an austere religious sect, whose members "…renounced the pleasures of this world, for the earth and all that it held to them was but a kind of illusion, and the true reality was the New Jerusalem toward which they were longing" [1]. Martine and Phillipa are the unmarried daughters of the founder of the religious sect who have a French maid-of-all-work, Babette, appearing from war-torn Paris under mysterious circumstances. Upon her arrival, the pious daughters are anxious to avoid any "… French luxury and extravagance" and therefore at the time explained that they "… were poor and that to them luxurious fare was sinful. Their own food must be as plain as possible". As it happens, their worries are allayed; and for next 12 years, Babette serves them such that the whole community come to acknowledge her excellence and depend on her quiet gifts. When Babette unexpectedly wins a princely sum of money in the French lottery, they become afraid she may leave them. Accordingly, against their better judgement, the sisters agree that Babette may cook them a special dinner celebrating the 100th anniversary of the sect's founding father. Unbeknownst to the sisters, Babette used to be a cordon bleu cook who prepares a sumptuous once-in-a-lifetime meal, leaving the guests questioning their lifelong denial of mortal pleasures.

In the novella, this cathartic meal is not described in much detail, following the vow of the devout and taciturn guests "… not to utter a word about the subject". In contrast, Danish director Gabriel Axel's Oscar-winning film adaptation tries hard to use visuals to convey the splendour of the dinner but still falls short of conveying the multisensory experience of a fine meal. Blixen is astute in using linguistic sparseness as a plot device, given that language, even that employed by great writers [2], very often fails to convey the exquisite sensory experiences of food upon which the story hinges. Blixen even feels moved to suggest that it is "… when man has not only altogether forgotten but has firmly renounced all ideas of food and drink that he eats and drinks in the right spirit". Language for all its powers is powerless when it comes to evoking the food's sensory routes to pleasure, yet the unity of pleasure is beautifully evoked: "Of what happened later in the evening nothing definite

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can here be stated. None of the guests later on had any clear remembrance of it. They only knew that the rooms had been filled with a heavenly light as if a number of small halos had blended into one glorious radiance. Taciturn old people received the gift of tongues; ears that for years had been almost deaf were opened to it. Time itself had merged into eternity. Long after midnight the windows of the house shone like gold, and golden song flowed out into the winter air".

Thus, Babette's feast becomes a route to intense well-being, and the pleasure is not just about the food but instead about providing unity and transcendence for the virtuous dinner guests who all leave the meal changed, suddenly awake to the potential of earthly pleasures.

For many years, such pleasures have remained mysterious and firmly within the domain of much great art. Yet, the advent of modern neuroscience has started to uncover some of the underlying mechanisms of associated brain changes.

This review describes what is known of the processing of food in scientific terms; from sensory identification of the uni- and multisensory properties of food to the associated prediction, memory and evaluation involved which may give rise to the experience of pleasure. Like all rewards, food depends on processing in interconnected and widespread brain regions to identify and characterise the different sensory properties and their multimodal integration. This processing is detailed in a multilevel model of the constituent processes involved in food intake over time. The focus here, however, is on the fundamental underlying brain mechanisms governing the initiation and termination of a meal leading to pleasure. Overall, the accumulated evidence shows that the pleasure evoked by food is remarkably similar to that of other rewards, suggesting a unitary pleasure system, whether engaging with food, sex, social or higher-order rewards. Food is thus not only highly pleasurable but also an excellent tool for discovering fundamental principles of brain function.

Brain principles of eating

While food clearly is essential to survival, it is the pleasure involved that makes eating worthwhile. While the members of the religious sect in Blixen's novella may try hard to deny the pursuit of pleasure in its many forms, their well-being is ultimately strongly enhanced as they submit to Babette's cooking, i.e. to the strong primal drive for pleasure. The evolutionary imperatives of survival and procreation are not possible without the principle of pleasure for the fundamental rewards of food, sex and conspecifics—and as such may well be evolution's boldest trick [3]. The scientific study of pleasure, *hedonia research*, is dedicated to searching for the functional neuroanatomy of hedonic processing, taking its name from the ancient Greek for pleasure (*ἡδονή; transl. hédoné*) derived from the word for "sweet" (*ἡδύς, transl. hēdús*) [4].

In the novella, the sect's initial food asceticism may stem from their religious beliefs but is guided by the basic homeostatic regulation of human eating behaviour [5], of which animal models have elucidated in great details the many subcortical circuits and molecules shared amongst mammals including humans [6-8]. Yet, as illustrated by the effects of Babette's Feast, homeostatic processes are not solely responsible for human eating. This *hedonic eating* is difficult to suppress and is even more poignantly illustrated by the current worldwide obesity pandemic [9]. There is often very little well-being linked to such over-eating, with *anhedonia*—the lack of pleasure—being a prominent feature of affective disorders. From this public health perspective, it is imperative that we better understand the fundamental pleasure systems such that we find new and more effective ways of re-balancing the system and potentially reducing obesity which is threatening to undermine public health [10].

Eating can seem simple but at its most basic, human food intake is still rather complex. The procurement of food can be surprisingly difficult in the wide variety of often hostile climates inhabited by humans. Once food is available, the preparation and eating of food are also complex processes, involving a multitude of peripheral and central processes for carefully orchestrated acts requiring significant brain processing. The necessary, sophisticated motivational, emotional and cognitive processing are likely to have been main drivers for the evolution of large primate brains [11]. The brain principles underlying eating have been investigated for a long time in many mammalian species [6,12]. Here, the focus is on the pleasure component of human eating, which over the last decade has started to transform our understanding [13,14].

To understand pleasure in the brain, it is important to consider the main challenge for the brain which is to successfully balance resource allocation for survival and procreation [15]. In order to achieve this balance, different rewards compete for resources over time. In understanding the multi-faceted nature of pleasure, it can therefore be useful to consider the typical cyclical time course shared between all rewards with distinct appetitive, consummation and satiety phases [16,17] (Figure 1). The research has demonstrated that pleasure consists of multiple brain networks and processes and involves a composite of several components: "liking" (the core reactions to hedonic impact), "wanting" (motivational processing of incentive salience) and learning (typically Pavlovian or instrumental associations and cognitive representations) [18-21]. These component processes have discriminable neural mechanisms, which wax and wane during the cycle. The neural mechanisms of *wanting*, *liking* and *learning* can occur at any time during the

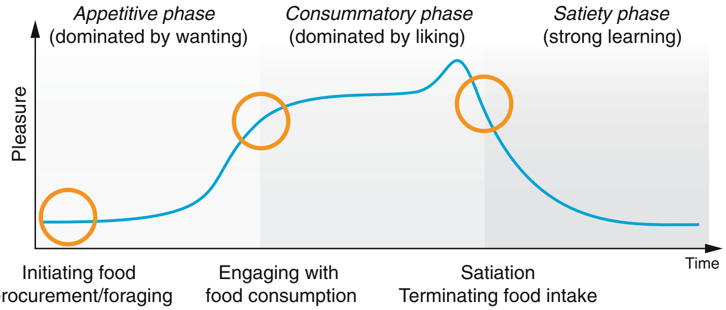

Figure 1 The pleasure cycle. The cyclical processing of rewards has classically been proposed to be associated with appetitive, consummatory and satiety phases [16,17]. Research has demonstrated that this processing is supported by multiple brain networks and processes, which crucially involves *liking* (the core reactions to hedonic impact), *wanting* (motivational processing of incentive salience) and *learning* (typically Pavlovian or instrumental associations and cognitive representations) [18-21]. These components wax and wane during the pleasure cycle and can co-occur at any time. Importantly, however, wanting processing tends to dominate the appetitive phase, while liking processing dominates the consummatory phase. In contrast, learning can happen throughout the cycle.

pleasure cycle, though wanting processes tend to dominate the appetitive phase (and are primarily associated with the neurotransmitter dopamine), while liking processes dominate the consummatory phase (and are associated with opioids) [13]. In contrast, learning can happen throughout the cycle (and is thought to be associated with synaptic plasticity). A neuroscience of pleasure seeks to map the necessary and sufficient pleasure networks allowing potentially sparse brain resources to be allocated for survival.

This basic cyclical model of pleasure can be expanded into an elaborate multilevel model of food intake taken in account the episodic and tonic changes over time (Figure 2) [12]. The model links the pleasure cycle with the cyclical changes in hunger levels related to the initiation and termination of meals and the way food intake

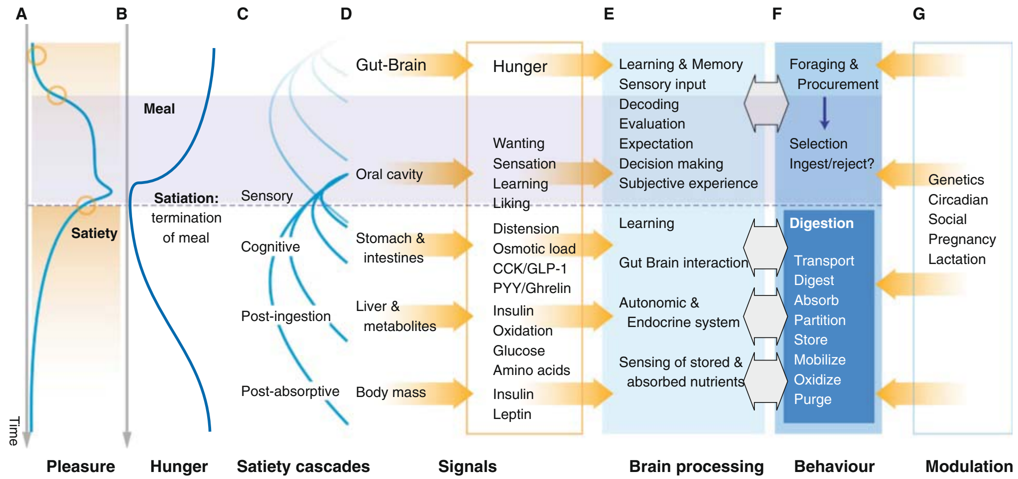

Figure 2 Multilevel model of food intake over time. The control of eating over time involves many different levels of processing as illustrated by the food. The changes at each level before, during and after meals are shown in each column which summarises the episodic and tonic changes over time (moving from top to bottom): **A)** pleasure cycle, **B)** the levels of hunger, **C)** satiation/satiety cascade (sensory, cognitive, post-ingestion and post-absorptive signals), **D)** origin of signals (gut-brain, oral cavity, stomach and intestines, liver and metabolites and body mass) and signal carriers, **E)** brain processing, **F)** behavioural changes including digestive system and **G)** general modulatory factors (see text for further information) [12].

comes about through the interaction given signals from the body, e.g. from the brain, gut-brain, oral cavity, stomach and intestines, liver and metabolites and body mass.

The dual processes of satiation and satiety are central to the model and to the energy obtained by the associated meals [22]. Terminating eating is complex process, which is encapsulated by *satiation* [23], while *satiety* is the feeling of fullness that persists after eating to suppress further eating. These processes are controlled by a cascade of sensory, cognitive, post-ingestion and post-absorptive signals, beginning with the consumption of a food in a meal and continuing as the food is digested and absorbed.

The multilevel model of food intake describes the changes over time in A) pleasure, B) the levels of hunger, C) satiation/satiety cascade signals, D) origin of signals and signal carriers, E) brain processes, F) behavioural changes including those in the digestive system and G) general modulatory factors (Figure 2). Many of these changes have been described elsewhere, e.g. the mechanisms of the changes after the termination of a meal such as the gut-brain interactions, include signals from receptors in the digestive tract which are sensitive to calorie-rich nutrients (even in the absence of taste receptors) [24,25].

Here, however, the focus is on the processing principles involved primarily in the initiation and termination of a meal (Figure 3). The multisensory experience of food intake involves all the senses with different routes into the brain; from the distant processing of sight, sound and tactile of food to more proximal smell, taste and tactile (mouth-feel) processing. Smell is the most important determinant of the flavour of food and comes to the brain via orthonasal and retronasal pathways, experienced as we breathe in and out, respectively [26]. As demonstrated by the case with coffee, the subjective olfactory experience can feel very different from smelling the coffee in the cup to tasting the coffee in the mouth, which also relies on pure tastants (such as bitter) and mouth feel factors (such as the smoothness of the crema) (Figure 3A).

This sensory information about food is coming from receptors in the body, typically the eyes, ears, nose and

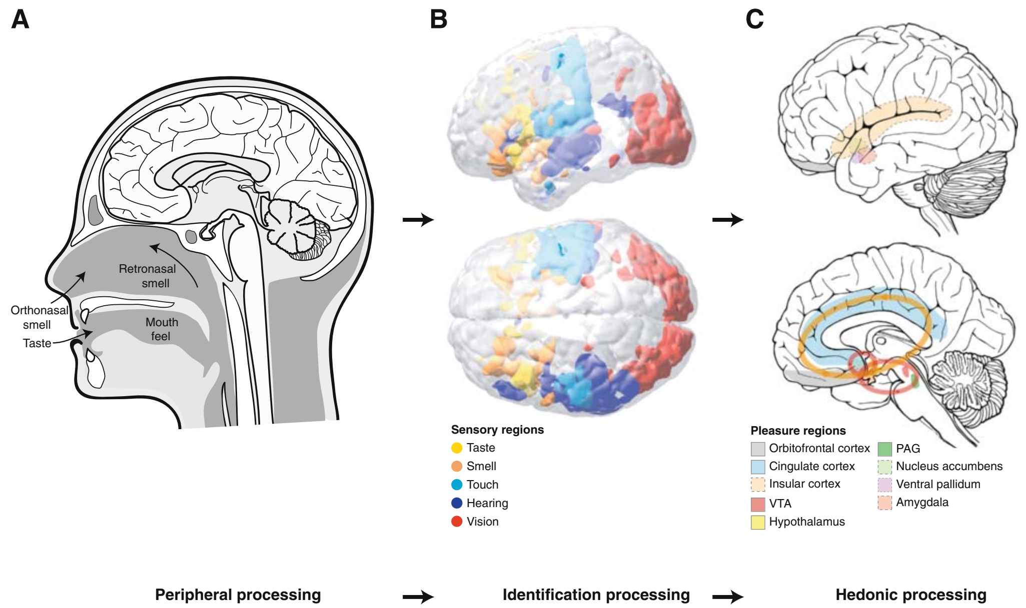

Figure 3 The pleasure of eating: from receptors to the brain. A) The multisensory experience of food intake involves all the senses with different routes into the brain from receptors in the body, typically the eyes, ears, nose and oral cavity: From the distant processing of sight, sound and tactile of food to more proximal smell, taste and tactile (mouth-feel) processing. Smell is the most important determinant of the flavour of food and comes to the brain via orthonasal and retronasal pathways, experienced as we breathe in and out, respectively. **B)** Remarkably similar topology is found between people with vision (red) always processed in the back of the brain, audition (dark blue) processed in regions of the temporal cortex, touch (light blue) in somatosensory regions, and olfaction (orange) and taste (yellow) in frontal regions. Importantly, unlike the other senses, olfactory processing is not processed via the thalamus, which may explain the hedonic potency of odours. **C)** The pleasure system includes the orbitofrontal cortex (grey), the cingulate cortex (light blue), the ventral tegmental area in the brainstem (light red), the hypothalamus (yellow), the periventricular grey/periacqueductal grey (PVG/PAG, green), nucleus accumbens (light green), the ventral pallidum (light purple), the amygdala (light red) and the insular cortices (not shown).

oral cavity and gets processed in the primary sensory cortices of the brain. The topology of these regions are remarkably similar between people with vision (red) always processed in the back of the brain, audition (dark blue) processed in regions of the temporal cortex, touch (light blue) in somatosensory regions and olfaction (orange) and taste (yellow) in frontal regions (Figure 3B). Importantly, unlike the other senses, olfactory processing is not processed via the thalamus which may explain the hedonic potency of odours [27]. Note that it is important that we are able to identify a food stimulus independently of whether we are hungry or sated, and accordingly, sensory information in primary sensory cortices is remarkably stable and not modulated by motivational state.

The sensory information is further integrated in multisensory areas before it is evaluated for reward value in the pleasure system. Here, the processing depends on prior memories, expectations and state and may give rise to brain activity which gives rise involuntary pleasure-evoked behaviour (such as licking of lips or soft moaning) and, at least in humans, subjective pleasure (Figure 3C).

Neuroscience has started to map the pleasure system in many species. This has been shown to include a number of important regions such as pleasure hotspot regions in subcortical areas of the brain such as the nucleus accumbens and ventral pallidum [28,29]. Manipulations of these regions with opioids have been shown to causally change pleasure-elicited reactions [13]. Other regions involved in pleasure have been found using human neuroimaging in the orbitofrontal, cingulate, medial prefrontal and insular cortices [30-37]. The pleasure system does not act in splendid isolation but is of course embedded within much larger brain networks. We are beginning to understand the metastable nature as well as the topological and functional features of these networks using advances in network science and graph theory together with advanced whole-brain computational models [38,39].

Computational processing principles for eating

Overall, eating has been demonstrated to rely on at least five fundamental processing principles: 1) hunger and attentional processing; 2) motivation-independent discriminative processing of identity and intensity; 3) learning-dependent multisensory representations; 4) reward representations of valence and 5) representations of hedonic experience [12,40]. In the following, these are briefly described.

Hunger and other attentional processing

Typically, changes in ongoing brain activity are driven by changes in the internal or external environment, signalling that the brain needs to start to reallocate resources and change behaviour. This motivational drive for change is strong for food intake, where hunger is a major attentional signal that along with other homeostatic signalling can influence the brain to initiate food-seeking behaviours, typically following the satiety phase from the previous meal. The hunger information comes primarily from gut-brain interactions signalling if the nutrients eaten in the previous meal have yielded the expected amount of energy but a large part is also played by habit (such as regular meal times) and learning, including social interactions which may lead to overeating due to diminished attention towards the food [41,42]. Signals from receptors in the gut and in the circulatory system are vital in initiating eating through conveying messages for the need of nutrients or energy uptake [6,43].

The healthy system is balanced through careful monitoring and learning throughout life. In the presence of sufficient nutrients, healthy adults are able to maintain a stable body weight by careful management of nutrient uptake, energy needs and the balance with energy expenditure [44]. In animal models, this homeostatic component has been shown to relate to activity in hypothalamic circuits including the arcuate nucleus [6,43]. Hedonic influences beyond homeostasis can lead to malfunction to this control of energy balance, e.g. leading to obesity, potentially through a mismatch between the expected pleasure compared to the actual energy uptake from food intake [11,45].

Motivation-independent processing of identity and intensity

It is vital that reliable sensory food information is provided for the brain to guide ingestion decision-making. Eating has to be controlled very carefully since erroneous evaluation of the sensory properties of foods can potentially be fatal if ingesting toxins, microorganisms or non-food objects. Mammals have been shown to have brainstem reflexes (stereotypical for each basic taste) that are based on rudimentary analyses of the chemical composition, and which are not altered, even by the loss of all neural tissue above the level of the midbrain [46]. Eating-related behaviours in humans and other animals can usefully be described as a strategy to maintain a balance between conservative risk-minimising and life-preserving strategies (exploitation) with occasional novelty seeking (exploration) in the hope of discovering new, valuable sources of nutrients [47].

The sensory information about the identity and intensity of a food—sometimes called a *flavour object*—reaching the primary sensory cortices appears to be motivation-independent [48]. This principle has been demonstrated by neurophysiological and neuroimaging experiments using five basic pure tastes of salt, bitter, sour, sweet and umami to locate the primary taste area in humans in the bilateral anterior insula/frontal operculum [49-53] (Figure 4). Please note that one study has reported changes in activity in the primary taste cortex by expectancy [54]; but unfortunately, the authors did not publish the

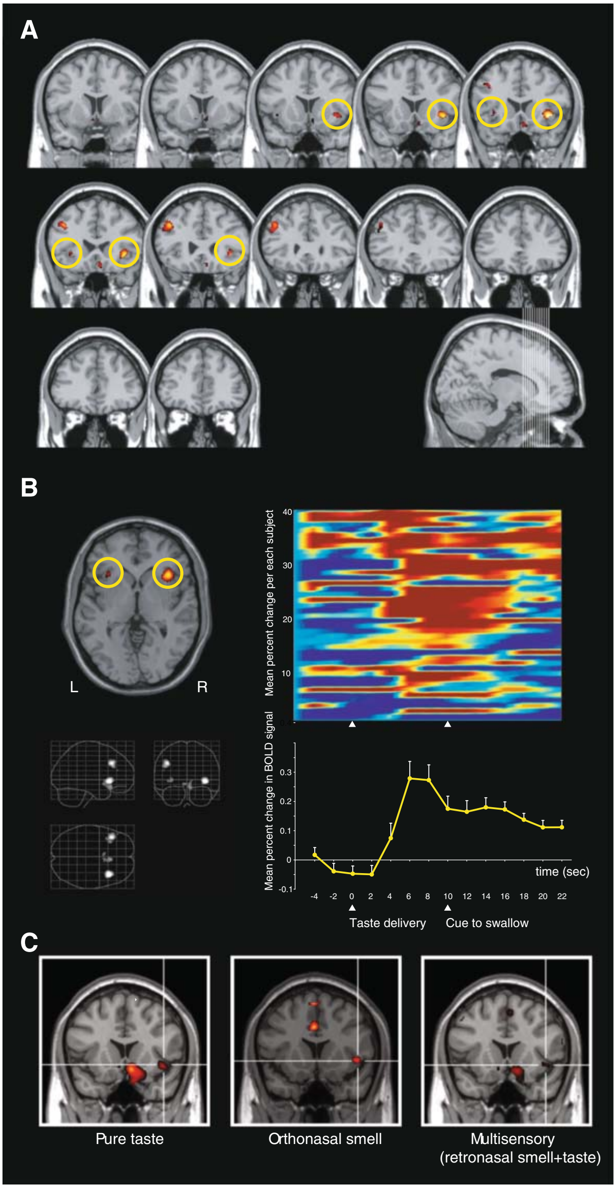

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Figure 4 Motivation-independent representations of food in primary sensory cortices. Pure taste is the archetypical reinforcer associated with food. **A)** Consistent with findings in non-human primates, neuroimaging has located the primary human taste cortex in bilateral anterior insular/frontal opercular cortices (yellow circles) with peak MNI coordinates of [x, y, z: 38,20,–4] and [x, y, z: −32,22,0] [53]. **B)** This data is based on 40 datasets from four experiments using eight unimodal and six multimodal taste stimuli ranging from pleasant to unpleasant. Each small aliquot of 0.75 mL taste stimulus was delivered via polythene tubes to the mouth of the participant who was asked to move it around before being cued to swallow after typically 10 s. To properly control and rinse out the effects of each stimulus, the taste stimulus was followed by a tasteless solution with the main ionic components of saliva. The time course of blood oxygen-level detection (BOLD) activity in right primary taste cortex is shown for all 40 subjects (top) and averaged across all (bottom) (for taste minus tasteless solution). **C)** Multisensory sensory integration was found in a region of the anterior insular cortex which responded to pure taste, orthonasal smell and flavour (retronasal smell and taste) [63].

exact coordinates of their putative primary taste cortex. It is thus difficult to trust this finding which is further undermined by visual inspection of the published figure, which clearly shows that the authors' purported primary taste cortex is located significantly posterior in the medial insular cortex, in contrast to the anterior insular primary taste region reported above and in all other careful neuroimaging taste studies.

Learning-dependent multisensory representations

Food-related decision-making depends on the integration of multisensory information about the food which includes information about temperature, viscosity, texture, fat contents, pungency and irritation mediated by a large variety of neural systems [25]. Neuroimaging this learning-dependent multisensory integration has found that the human orbitofrontal cortex integrates information from auditory [55], gustatory [51], olfactory [56], somatosensory [57] and visual [58] inputs, as well as information from the visceral sensory system [59]. The role of expectation and motivational control of appetite has also been investigated using restaurant menus which also found engagement of the orbitofrontal cortex [60] [61].

These human findings are consistent with neurophysiological recordings showing that the non-human primate orbitofrontal cortex receives input from all of the five senses [62]. These sensory inputs enter the orbitofrontal cortex primarily through its posterior parts and are integrated in more anterior areas [34]. The interaction between taste and smell revealed by neuroimaging is found in the orbitofrontal cortex and nearby agranular insula (Figure 4C) [33,50,63].

Reward representations of sensory stimuli

Subsequent to establishing motivation-independent representations and multisensory representations of information about a food, affective valence is assigned, helping to guide prediction and decision-making. Again, pure taste serves as a good example with a neuroimaging study finding a dissociation between the brain regions responding to the intensity of the taste and its affective valence [64]. Another study found that subjective ratings of taste pleasantness correlated with activity in the medial orbitofrontal cortex (medial OFC) and in the anterior cingulate cortex [65] but, importantly, not with activity in the primary taste region, which was motivation-independent. Further evidence comes from experiments using orthonasal olfaction to show dissociable encoding of the intensity and pleasantness of olfactory stimuli, with the intensity encoded in the amygdala and nearby regions, and the pleasantness correlated with activity in the medial OFC (Figure 5A) and anterior cingulate cortex [66-68].

These reward-related findings in the medial OFC cohere with neuroimaging studies using other rewards. One study found a correlation between activity in the medial OFC with the amount of monetary wins and losses [69] (Figure 5B). Similarly, the subjective experience of methamphetamine over minutes was found to correlate with activity in the medial OFC [70] (Figure 5C). Even studies on the much shorter timescales of milliseconds have found activity in the medial OFC related to the reward of images of cute babies [71] (Figure 5D). These results point to the unity of reward-related activity in the pleasure system across many different rewards, which in turn suggest a system with a common currency of reward. Such a system would make it easier to decide and choose between different rewards.

Representations of hedonic experience

Finally, the evidence suggests that the subjective hedonic experience of food is encoded in activity in the pleasure system. In humans, the mid-anterior orbitofrontal cortex (mid-OFC) appears to be a key region as demonstrated by a selective-satiety neuroimaging study where activity in this region shows not only a selective decrease in the reward value to the food eaten to satiety (and not to the food not eaten) but also a correlation with pleasantness ratings (Figure 5E) [33]. This result indicates that the reward value of the taste, olfactory and somatosensory components of a food are represented in the orbitofrontal cortex and, therefore, that the subjective pleasantness of food might be represented in this region. Other studies have supported this finding, including an experiment investigating true taste synergism, where the intensity of a taste is dramatically enhanced by adding minute doses of another taste. The strong subjective enhancement of the pleasantness of umami taste that occurs when 0.005 M inosine 5′-monophosphate is added to

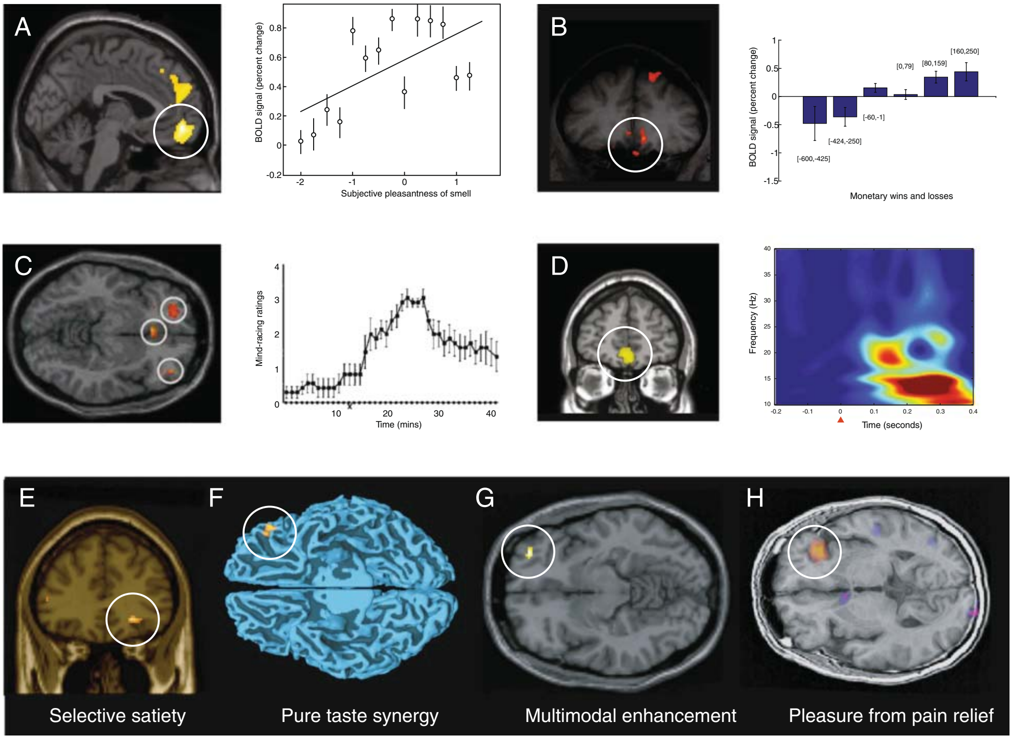

Figure 5 Reward in the human orbitofrontal cortex (OFC). Neuroimaging studies have revealed that the OFC is a heterogeneous brain region, where the different parts are engaged in different aspects of reward. Here, the focus is on the difference between activity in the medial OFC, which appears to monitor and evaluate the reward value **(A–D)**, while the mid-anterior OFC (mid-OFC) contains activity encoding the subjective experience of pleasure **(E–H)**. A) The activity in medial OFC is correlated with subjective ratings of pleasant and unpleasant smell [66]. B) Similarly, the activity in medial OFC is correlated with monetary wins and losses with no behavioural consequences [69]. C) Activity in the medial OFC is also tracking reward value over time, as shown in a neuroimaging study of the changing over minutes of pleasure of methamphetamine in drug-naïve participants [70]. D) The medial OFC also tracks the reward value of cute baby faces on faster timescales over milliseconds within 130 ms [71]. E) In contrast, activity in mid-OFC correlates with the subjective pleasure of food in a study of selective satiety [33]. F) Similarly, a study of supra-additive effects of pure taste combining the umami tastants monosodium glutamate and inosine monophosphate found subjective synergy effects in mid-OFC [72]. G) The synergy of supra-additive effects combining retronasal odour (strawberry) with pure sucrose taste solution was found in the mid-OFC [65]. H) Further, mid-OFC also became active when using deep brain stimulation in the PAG for the relief of severe chronic pain [73].

0.5 M monosodium glutamate (compared to both delivered separately) correlated with increased activity in mid-OFC (Figure 5 F) [72]. Similarly, investigations of the synergistic enhancement of a matched taste and retronasal smell found significant activity in the same mid-OFC region (Figure 5G) [63]. These food-related hedonic findings fit well with evidence coming from the study of other pleasures, including the finding of significant activity in mid-OFC in a study using magnetoencephalography (MEG) with deep brain stimulation to investigate the pleasurable relief from severe chronic pain (Figure 5H) [73].

Conclusions

As demonstrated poignantly by *Babette's Feast*, food is not only an important part of a balanced diet; it is also one of our main routes to pleasure. The novella opens many interesting question with regard to well-being and the good life and in particular shows that to allow oneself to be open to the possibility of pleasure of food is also allowing for the deep experiences of the multitude of pleasures. This is in sharp contrast to the denial of the pleasure of food leading to anhedonia, the lack of pleasure, which is a key constituent component of affective disorders.

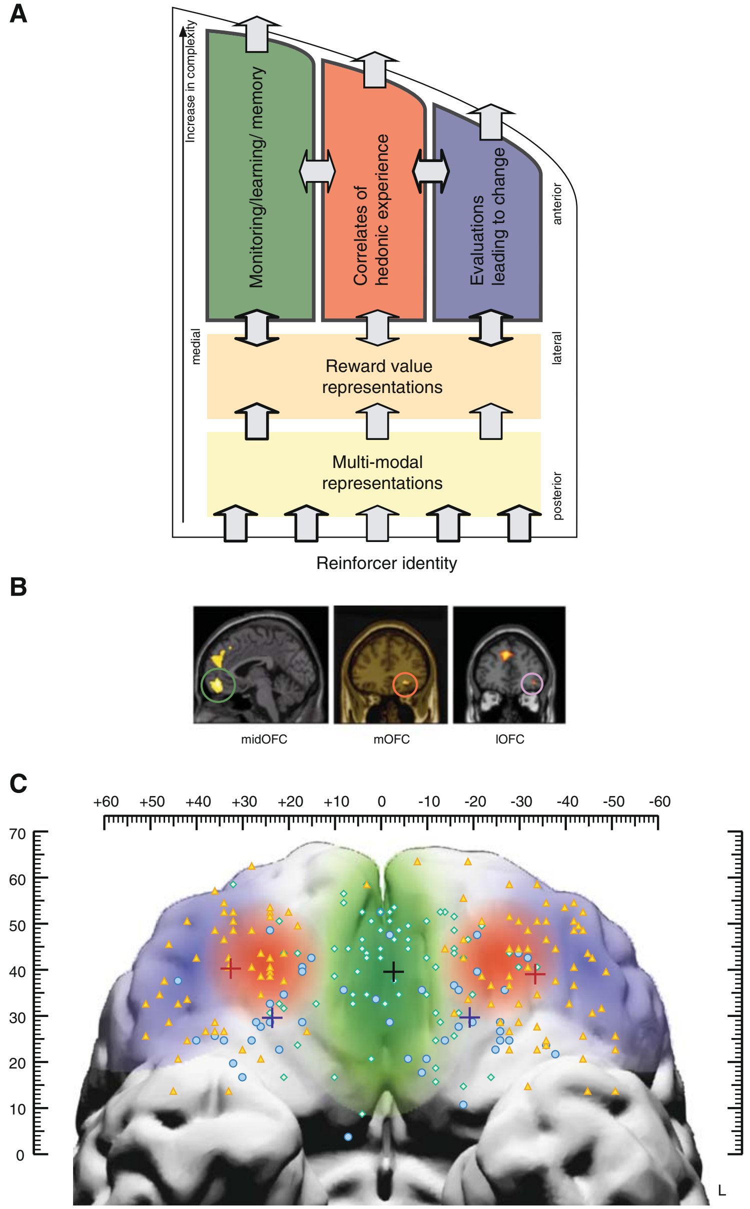

Figure 6 (See legend on next page.)

(See figure on previous page.)

Figure 6 Model of information flow in the orbitofrontal cortex (OFC). The spatial heterogeneity of the human OFC has been revealed with neuroimaging. **(A-C)** The OFC is involved in most of the phases of the pleasure cycle, including evaluation, expectation, experience as well as decision-making and selection. Sensory information comes to the OFC where it is available for pattern association between primary (e.g. taste) and secondary (e.g. visual) reinforcers. Sensory information is combined in multisensory representations in the posterior OFC with processing increasing in complexity towards more anterior areas. The reward value of reinforcers is assigned in more anterior regions. This information is stored for valence monitoring/learning/memory (in medial OFC, green) and made available for subjective hedonic experience (in mid-OFC, orange) and used to influence subsequent behaviour (in lateral OFC with links to regions of anterior cingulate cortex, blue). The OFC participates in multiple modulatory brain-loops with other important structures in the pleasure system such as the nucleus accumbens, ventral pallidum, amygdala and hypothalamus, as well as modulation with autonomic input from the gut. [34]. B) Examples of monitoring reward value in medial OFC (green) was found in a study of orthonasal smell where the activity correlated with subjective ratings of pleasant and unpleasant smell [66]. Activity in mid-OFC (orange) correlates with the subjective pleasure of food in a study of selective-satiety [33]. In contrast, the activity in lateral OFC (shown in red) was found when changing behaviour in a rapid context-dependent reversal task of simple social interactions [84]. C) A large meta-analysis of neuroimaging studies confirmed the differential functional roles of these regions [34]. Future avenues of research include describing temporal unfolding of activity, similar to early involvement of the medial OFC (<130 ms) in processing rewards such as cute babies and guide attentional resources [71].

The science of pleasure has made great strides in recent years [4], due not in small parts to using food as a pleasure-eliciting stimulus. As demonstrated in this review, the research has uncovered many of the fundamental brain mechanisms governing eating and pleasure in general. It has helped understand the brain's complex resource allocation problems with food competing with other rewards for time and resources. In particular, the brain must make important decisions of how best to balance exploration and exploitation to ensure survival. These decisions involve deciding when to pursue a reward, and whether to initiate, sustain and terminate the wanting, liking and learning processes involved in the different phases of the pleasure cycle (Figure 1). Eating is a complex process that involves many different factors over time as described in a multilevel model (Figure 2). The model demonstrates the cyclical changes in hunger levels related to the initiation and termination of meals, as they relate to signals from the brain, gut-brain, oral cavity, stomach and intestines, liver and metabolites and body mass.

Here, the focus has been on the computational principles for the multisensory processing of food information that initiates and terminates a meal, as well as the pleasure involved (Figure 3). Five main processing principles were discussed: 1) hunger and attentional processing; 2) motivation-independent processing of identity and intensity (Figure 4); 3) learning-dependent multisensory representations; 4) reward representations and 5) representations of hedonic experience. These principles are implemented within the orbitofrontal cortex that is a key, heterogeneous region in the pleasure system (Figures 5 and 6).

Furthermore, pleasure research has shown that food, sex and social interactions are fundamental to our survival and these basic stimuli take priority in resource allocation. It has also shown the unity of pleasure processing of different rewards, with food, sex, social and higher-order stimuli (such as music and money) in a unified pleasure system [12,13,74-76,84].

Much remains to be done, but finally science has gained a toehold in understanding how pleasure can come to transform lives. Understanding the pleasure of food has played a major part in hedonia research and may even offer some insights into well-being. We have previously taken a lead from Aristotle's distinction between *hedonia* and *eudaimonia* (a life well-lived) to show how the study of pleasure may offer some insights into well-being [77].

Gastronomy offers the potential to expand on these findings and create exciting experiences and great pleasure. The rise of molecular gastronomy and gastrophysics have afforded chefs with unprecedented control over the production of novel flavours and textures of food [78,79]. These experiences are by their very nature multisensory and like all experiences highly dependent on expectation and prior experiences [80]. Using scientific tools and insights allows playful chefs to create unique and highly pleasurable dining experiences, e.g. using touch and sound as interesting extras in their gastronomical palette [81]. Yet, all foods are ultimately dependent on the state of the diner's brain and body [82], and the emergence of the neuroscience of the pleasure of gastronomy could help guide further progress [11,83]. Both the science and art of cooking stand to benefit much from future collaborations between scientists and chefs, especially in so far this research can help increase the pleasure of eating and well-being.

Babette's Feast shows how a sumptuous dinner can bring about much pleasure and transform lives. Babette uses all her money and skills on creating the once-in-a-lifetime dinner, yet at the end she tells the sisters: "A great artist, Mesdames, is never poor. We have something, Mesdames, of which other people know nothing". While it is true that creating great art takes skills and years of practice, it is also important to remember that every moment and every bite of food carries within it the possibility of pleasure. The brain is built for pleasure and it is through learning to appreciate the extraordinary in ordinary experiences, through pursuing the variety of pleasures rather than the relentless single-minded pursuit (hedonism) or denial of pleasure (asceticism) that a life well-lived can be constructed.

Competing interests
The author declares that he has no competing interests.

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Flavour

REVIEW Open Access

Eating with our ears: assessing the importance of the sounds of consumption on our perception and enjoyment of multisensory flavour experiences

Charles Spence

Abstract

Sound is the forgotten flavour sense. You can tell a lot about the texture of a food—think crispy, crunchy, and crackly—from the mastication sounds heard while biting and chewing. The latest techniques from the field of cognitive neuroscience are revolutionizing our understanding of just how important what we hear is to our experience and enjoyment of food and drink. A growing body of research now shows that by synchronizing eating sounds with the act of consumption, one can change a person's experience of what they think that they are eating.

Keywords: Sound, Flavour, Crunchy, Crispy, Crackly

Review

Introduction

Try eating a crisp (or potato chip) without making a noise. It is, quite simply, impossible! The question to be addressed in this article concerns the role that such food-related eating sounds play in the perception of food or drink. Do you, for example, think that your experience of eating a crispy, crunchy, or crackly food differs as a function of whether you find yourself at a noisy party, or while listening to loud white noise (if you happen to find yourself in a psychologist's laboratory; [1])? The sounds that we hear when we eat and drink, and their impact on us, constitute the subject matter of this article.

In the pages that follow, I hope to convince you that what we hear when we bite into a food or take a sip of a drink—be it the crunch of the crisp or the fizz of the carbonation in the glass—plays an important role in our multisensory perception of flavour, not to mention in our enjoyment of the overall multisensory experience of eating or drinking. What we hear can help us to identify the textural properties of what we, or for that matter anyone else, happens to be eating: How crispy, crunchy, or crackly a food is or even how carbonated the cava. Importantly, as we will see below, sound plays a crucial role in determining how much we like the experience. Indeed, it turns out that crispness and pleasantness are highly correlated when it comes to our rating of foods [2]. That said, many of my academic colleagues would rather restrict the contribution of sound to a minor modulatory role in texture perception.[a] And, as we will also see in a moment, some firmly believe that what we hear has *absolutely nothing* to do with the perception of flavour. In this article, I hope to convince you otherwise.

I would argue that the *zeitgeist* on this issue is slowly starting to change. I have certainly noticed a number of my scientific colleagues tentatively including sound as one of the senses that can impact on the experience of food and drink. For instance, Stevenson ([3], p. 58) believes that crispness is a flavour quality. A number of researchers now acknowledge the fact that the sound of consumption is an important factor affecting the consumers' experience of food and drink [4,5]. And, as we will see later, food sounds have a particularly noticeable influence on people's perception of crispness [2,6]. A growing number of chefs are now considering how to make their dishes more sonically interesting, using everything from a sprinkling of popping candy through to using the latest in digital technology (see [7,8], for reviews).

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I want to take a look at the older research on food sounds as well as the latest findings from the gastrophysics lab. The evidence concerning the contribution of audition to crispy, crunchy, crackly, carbonated, and creamy sensations will be reviewed. I will then go on to illustrate how the cognitive neuroscience-inspired approach has revolutionized our understanding in this area over the last decade or so.

Auditory contributions to flavour perception

The majority of reviews on the topic of multisensory flavour perception either do not talk about audition or else, if they do, provide only the briefest mention of this 'forgotten' flavour sense. I have looked at a number of representative review articles and books on flavour that have been published over the decades (and which are arranged chronologically below) and tallied-up just how much (or should that not be how little) coverage the authors have given over to hearing. The percentages tell their own story: Crocker [9] 0%; Amerine, Pangborn, and Roessler [10] <1%; Delwiche [11] 3%; Verhagen and Engelen [5] <1%; Stevenson [3] 2%; Shepherd [4] 1%; and Stuckey [12] 4% (these percentages were calculated by dividing the number of book pages given over to audition by the total number of book pages. Note that if each of the five senses were given equal weighting, then you would expect to see a figure closer to 20%). One could all too easily come away from such literature reviews with the distinct impression that what we hear simply does not play any significant role in our experience of food and drink. How else to explain the absence of material on this sense. Delwiche ([11], p. 142) seems to have captured the sentiment of many when she states that '*While the definitive research remain* [sic] *to be done, the interaction of sound with the chemical senses seems unlikely*'.

Indeed, the downplaying of sound's influence would appear to be widespread amongst both food professionals and the general public alike [13,14]. For instance, when 140 scientists working in the field of food research were questioned, they rated 'sound' as the *least* important attribute contributing to the flavour of food, coming in well behind taste, smell, temperature, texture appearance, and colour (see Table 1). Furthermore, sound also came in as the least essential and most changeable sense where flavour was concerned. I believe that these experts are all fundamentally underestimating the importance of sound.

The results of another study [14] highlight that similar opinions are also held by regular consumers as well. Eighty people without any special training or expertise in the food or beverage sector were asked to evaluate the relative importance of each of the senses to a wide range of products ($N = 45$), including various food and drink items. Interestingly, regardless of the product category, audition was rated as the *least* important of the senses (see Table 2). Perhaps it should come as no surprise, then, to find that auditory cues also fail to make it into the International Standards Organization definition of flavour (see [15,16]). Indeed, according to their definition, flavour is a '*Complex combination of the olfactory, gustatory and trigeminal sensations perceived during tasting. The flavour may be influenced by tactile, thermal, painful and/or kinaesthetic effects*'.

One thing to bear in mind here though is that there is actually quite some disagreement in the field as to how 'flavour' should be defined (e.g. [11,17]). While some researchers would prefer that the term be restricted to gustation, retronasal olfaction, and possibly also trigeminal inputs (see, for example, [15,16]), others have suggested that the senses of hearing and vision should also be incorporated [4,5,18-20]. There is no space to get into the philosophical debate surrounding this issue here (the interested reader is directed to [21]). In this article, I will use the term 'flavour' in a fairly broad sense to mean, roughly, 'the overall experience of a food or beverage' (see [5], for a similar position). As such, the consumer's perception of the oral-somatosensory and textural properties of a foodstuff will be treated as a component part of their flavour experience (though see [11], for a different position).

The traditional view (that sound has little role to play in our flavour experiences) contrasts with the position adopted by a number of contemporary modernist chefs such as Heston Blumenthal who, for one, is convinced that you need to engage *all* of a diner's senses if you want to create truly memorable dishes. Just take the following quote from the cover sheet of the tasting menu at The Fat Duck restaurant in Bray: '*Eating is the only thing we do that involves all the senses. I don't think that we realize just how much influence the senses actually have on the way that we process information from mouth*

Table 1 Summary of the opinions of 140 experts concerning the importance of various sensory attributes to flavour showing in what little regard sound is considered (adapted from [13])

	Taste	Smell	Temperature	Texture	Colour	Appearance	Sound
% Important	97	94	78	64	40	37	21
% Essential	96	90	37	34	12	16	6
% Changeable	0	2	19	41	68	68	82

Table 2 Results of a study demonstrating that even regular consumers pay surprisingly little attention to what they hear while eating and drinking (Source: [14])

	Vision	Touch	Audition	Smell	Taste
Food and drink	4.2	3.1	1.7	4.2	4.9
Soft drink	3.9	2.5	1.9	4.1	4.9
Cheese	4.1	3.3	1.5	4.3	4.9
Apple	4.4	3.8	1.9	3.8	4.9
Meats	4.5	2.9	1.5	4.5	4.8
Cookies	4.1	3.3	1.9	4.3	4.9

The results (mean ratings are shown) of a study in which 80 participants were asked 'How important is it to you how a [product] feels/smells/sounds/looks/tastes?' on a 5-point category scale (1 = very unimportant, 2 = unimportant, 3 = not important/not unimportant, 4 = important, and 5 = very important).

to brain'. (see http://www.fatduck.co.uk). Ferran Adrià seems to have been taking a similar line when he said that '*Cooking is the most multisensual art. I try to stimulate all the senses*' [22].

The last few years have seen something of a renaissance of interest in this heretofore neglected 'flavour' sense [23-25]. The crucial point to bear in mind here is that it turns out that most people are typically unaware of the impact that what they hear has on how they perceive and respond to food and drink. Consequently, I would argue that intuition and unconstrained self-report, not to mention questionnaires asking about the role of audition in flavour, are unlikely to provide an altogether accurate assessment of the sense's actual role in our multisensory experiences (whether or not those experiences relate to food or drink). Indeed, the decades of research from experimental psychologists have shown that the kinds of responses one gets from direct questioning rarely provide particularly good insights into the true drivers of people's behaviour, especially when one is looking at the interaction between the senses that gives rise to multisensory perception [26-28]. This means that we will need to focus on the results of well-designed empirical studies using more objective psychophysical measures in order to highlight the relative importance of the various factors/senses that really influence flavour perception in us humans.

Why think that what we hear is so much more important than we intuitively believe?

There are several lines of evidence pointing to the importance of sound to our food and drink experiences. In one early study, for instance, Szczesniak and Kleyn [29] reported that consumers mentioned 'crisp' more than any other descriptor in a word association test in which they had to list four descriptors in response to each of 79 foods. Now, while you might imagine that crispness is strictly a tactile attribute of food and, hence, that such results provide evidence for the importance of oral-somatosensation to our experience of food, the fact of the matter is that auditory cues play a key role in the delivery of this sensation [6]. These authors went so far as to suggest that crispness was an auditory sensation. Many chefs also appear to have texture top of mind: Just take three of the sensations that spring into the mind of the North American chef, Zakary Pelaccio, while eating: crispy (nicely fried chicken skin), fresh and crispy (raw veggies and herbs), and crunchy (corn nuts) ([30] p. 9).

Back in 2007, researchers from the University of Leeds came up with an equation to quantify just how important the crispness of the bacon, especially the sound of the crunch, is to the perfect BLT sandwich (see [31], pp. 79–80). Crucially, crispness was rated as the key element in creating the ideal offering. Dr. Graham Clayton, the lead researcher on the project, stated that '*We often think it's the taste and smell of bacon that consumers find most attractive. But our research proves that texture and the crunching sound is just – if not more – important*' [32].

Another example of the unrecognized importance of sound comes from the following anecdote: Some years ago, researchers working on behalf of Unilever asked their brand-loyal consumers what they would change about the chocolate-covered Magnum ice cream (a product that first appeared on the shelves in Sweden back in 1989). A frequent complaint that came back concerned all of those bits of chocolate falling onto the floor and staining one's clothes when biting into the ice cream. This feedback was promptly passed back to the product development team who set about trying to alter the formulation so as to make the chocolate coating adhere to the ice cream better. In so doing, the distinctive cracking sound of the chocolate coating was lost. And when the enhanced product offering was launched, consumers complained once again. It turned out that they did not like the new formulation either. The developers were confused. Had not they fixed the original problem that consumers had been complaining about. Nevertheless, people simply did not like the resulting product. Why not? Were consumers simply being fickle? In this case, the answer was no—though the story again highlights the dangers of relying on subjective report.

Subsequent analysis revealed that it was that distinctive cracking sound that consumers were missing. It turned out that this was a signature feature of the product experience even though the consumers (not to mention the market researchers) did not necessarily realize it. Ever since, Unilever has returned to the original formulation, thus ensuring a solid cracking sound every time one of their customers bites into one of their distinctive ice cream bars.

In fact, once you realize just how important the sound is to the overall multisensory experience, you start to understand why it is that the food marketers spend so much of their time trying to accentuate the crispy, crunchy, and crackly sounds in their advertisements [33]. I, for one, am convinced that the chocolate crackling sound is accentuated in the Magnum adverts [34,35]. Obviously, you want to make sure that you get the sensory triggers just right if you happen to be selling 2 billion of these ice creams per year (http://alvinology.com/2014/05/25/magnum-celebrates-25-years-of-pleasure/). Certainly, there is lots of talk of 'cracking chocolate' in online descriptions of the product (http://www.mymagnum.co.uk/products/) and in blogs: '*I experienced the crack of the chocolate while biting into it and the "mmmmm" sound in my mind while eating the ice-cream. I was lost into it :) It was pure pleasure indeed*'. (http://rakshaskitchen.blogspot.com/2014/02/magnum-masterclass-with-kunal-kapur.html).

Listen carefully enough and I think that you can often tell that the informative sounds of food consumption appear to have been sonically enhanced in many of the food ads seen on TV. A few years back, a Dutch crisp manufacturer named Crocky took things even further. They ran an advert that specifically focused on the crack of their crisps. The sound was so loud that it appeared to crack the viewer's television screen when eaten on screen [36].

Why do people like crispy so much?

Crispness is synonymous with freshness in many fruits and vegetables. Indeed, lettuce is the first food that comes to the mind of many North Americans when asked to name examples of crispy foods [37]. Other foods that people often describe as especially crispy include tortilla chips and, perhaps unsurprisingly, crisps [38]. The link with freshness is thought to be part of the evolutionary appeal of crisp and crunchy foods [33,39]. That said, for some people, these sonic-textural attributes have become desirable in their own right, regardless of their link to the nutritional properties of food. Why else, after all, are crisps so popular? It certainly cannot be for nutritional content nor is the flavour all that great when you come to think about it. Rather, the success of this product is surely *all* about the sonic stimulation—the crispy crunch. Over the years, a large body of research has documented that the pleasantness of many foods is strongly influenced by the sounds produced when people bite into them (e.g. [2,6,40,41]).

Summarizing what we have seen in this section, while most people—food scientists and regular consumers alike—intuitively downplay (disregard, even) the contribution of sound when thinking about the factors that influence their perception and enjoyment of food, several lines of evidence now hint at just how important what we hear really is to the experience of what we eat (and presumably also to what we drink).

A brief history of the study of the role of hearing in flavour perception

It was during the middle decades of the 20th Century that food scientists first became interested in the role of audition (see [42-44], for early research). In these initial studies, however, researchers tended to focus their efforts on studying the consequences, if any, of changing the background noise on the perception of food and drink (see [1], for a review). Within a decade, Birger Drake had started to analyze the kinds of information that were being conveyed to the consumer by food chewing and crushing sounds. Drake was often to be found in the lab mechanically crushing various foods and recording the distinctive sounds that were generated prior to their careful analysis [40,45-48]. Perhaps the key finding to emerge from his early work was that the sounds produced by chewing or crushing different foods varied in terms of their amplitude, frequency, and temporal characteristics.

Thereafter, Zata Vickers and her colleagues published an extensive body of research investigating the factors contributing to the perception of, and consumer distinction between, crispness and crunchiness (not to mention crackliness) in a range of dry food products (e.g. [41,49-54]; see [6,55], for reviews of this early research; and [56], for a more recent review). Basically, she found that those foods that are associated with higher-pitched biting sounds are more likely to be described as 'crispy' than as 'crunchy' ([55,57,58]; see also [59,60]). To give some everyday examples of what we are talking about here (at least for those in the English-speaking world): Lettuce and crisps are commonly described as crisp, whereas raw carrots, croutons, Granola bars, almonds, peanuts, etc. are all typically described as crunchy. Crispy foods tend to give off lots of high-frequency sounds above 5 kHz. By contrast, analyze the acoustic energy given off while munching on a raw carrot and you will find lots of acoustic energy in the 1–2 kHz range instead.

To date, crackly sensations have not received anything like as much attention from the research community. That said, crackly foods can typically be identified by the sharp sudden and repeated bursts of noise that they make [61]. Masking these sounds leads to a decrease in perceived crackliness. It turns out that the number of sounds given off provides a reasonably good measure of crackliness. Good examples of foods that make a crackly sound include pork scratchings or the aptly named pork crackling.

Despite all of the research that has been conducted in this area over the years, it is still not altogether clear just how distinctive 'crisp' and 'crunchy' are as concepts to many food scientists, not to mention to the consumers they study [62,63]. Certainly, the judgments of the crispness, crunchiness, and hardness of foods turn out to be very highly correlated [41]. Part of the problem here seems to be linguistic. Different languages just use different terms, or else simply have no terms at all, to capture some of these textural distinctions: To give you some idea of the problems that one faces when working in this area, the French describe the texture of lettuce as craquante (crackly) or croquante (crunchy) but not as croustillant, which would be the direct translation of crispy [59,64]. Meanwhile, the Italians use just a single word 'croccante' to describe both crisp and crunchy sensations.

Matters become more confusing still when it comes to Spanish speakers [63]. They do not really have their own words for crispy and crunchy, and if they do, they certainly do not use them[b]. Colombians, for instance, describe lettuce as 'frisch' (fresh) rather than as crispy. And when a Spanish-speaking Colombian wants to describe the texture of a dry food product, they either borrow the English work 'crispy' or else the French word 'croquante'. This confusion extends to Spain itself, where 38% of those questioned did not know that the Spanish term for 'crunchy' was 'crocante'. What is more, 17% of consumers thought that crispy and crunchy meant the same thing [63].

Of course, matters would be a whole lot simpler if there was some instrumental means of measuring the crispness/crunchiness/crackliness of a food. Then, we might not care so much what exactly people say when describing the sounds made by food products. However, it turns out that these are multisensory constructs, and hence, simply measuring how a food compresses when a force is applied to it provides an imperfect match to subjective ratings. A much better estimate of crispness, as perceived by the consumer, can be achieved not only by measuring the force-dependent deformation properties of a product but also by recording the sounds that are given off [51,65-67]. Taken together, these results suggest that the perception of crispness of (especially) crunchy foods (i.e. crisps, biscuits, cereals, vegetables, etc.) is characterized by tactile, mechanical, kinaesthetic, and auditory properties [50]. Of course, while it is one thing to demonstrate that the instrumental measures of crispness can be improved by incorporating some measure of the sound that the food makes when compressed, it is quite another to say that those sounds necessarily play an important role in the consumer's overall experience of a food [68]. And while Vickers and Bourne [6] originally suggested that crispness was primarily an acoustic sensation, Vickers herself subsequently pulled back from this strong claim [49].

One relevant piece of evidence here comes from Vickers [41] who reported that estimates of the crispness of various foods such as celery, turnips, and Nabisco saltines were the same no matter whether people heard someone else biting into and chewing these foods as if they themselves actually got to bite and chew them. Meanwhile, Vickers and Wasserman [69] demonstrated that loudness and crispness are highly correlated sensory dimensions (see also [66]).

Assessing the relative contribution of auditory and oral-somatosensory cues to crispness perception

The participants in a study by Christensen and Vickers [70] rated the crispness of various dry and wet foods using magnitude estimation and separately judged the loudness of the chewing sounds. These judgments turned out to be highly correlated both when the food fractured on the first bite ($r = 0.98$) and when it further broke down as a result of chewing ($r = 0.97$; see Figure 1). Interestingly, though, the addition of masking sounds did not impair people's judgments of the food. Such results were taken to suggest that both oral-somatosensory and auditory cues were (redundantly) providing the same information concerning the texture of the food that was being evaluated (though see also [1]).

Interim summary

Despite the informational richness contained in the auditory feedback provided by biting into and/or chewing a food, people are typically unaware of the effect that such sounds have on their multisensory perception or evaluation of particular stimuli (see also [71]). While the overall loudness and frequency composition of food-eating sounds are certainly two of the most important auditory cues when it comes to determining the perceived crispness of a food, it should be noted that the temporal profile of any sounds associated with biting into crispy or crunchy foods (e.g. how uneven or discontinuous they are) can also convey important information about the rheological properties of the foodstuff being consumed, such as how crispy or crackly it is [69].

The multisensory integration approach to flavour perception

The opening years of the 21st Century saw the introduction of a radically different approach to the study of flavour perception, one that was based on the large body of research coming out of neurophysiology, cognitive neuroscience, and psychophysics laboratories highlighting the profoundly multisensory nature of human perception. Originally, the majority of this literature tended to focus solely on the integration of auditory, visual, and tactile cues in the perception of distal events, such as the ventriloquist's dummy and beeping flashing lights (see [72,73], for reviews). However, it was not long before some of those straddling the boundary between

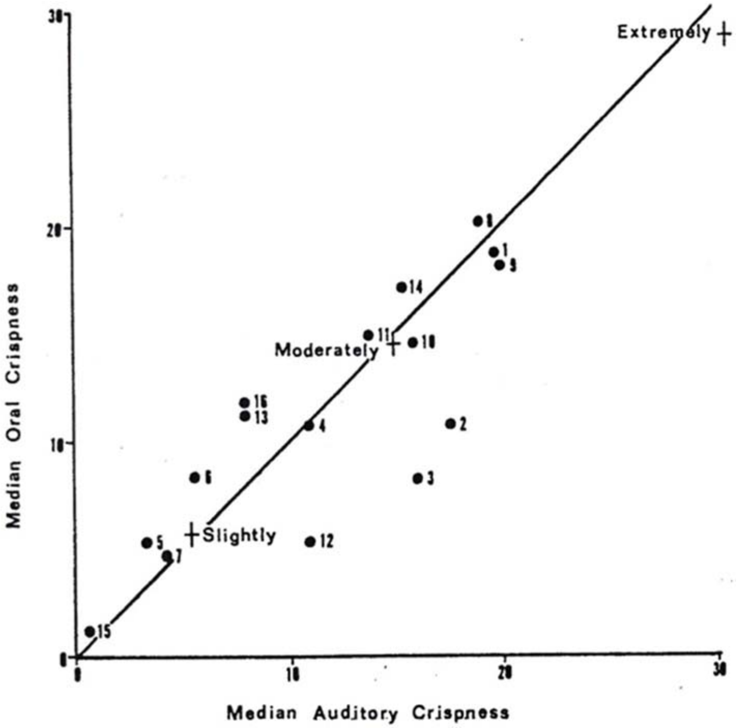

Figure 1 Graph showing the correlation between people's rating on the crispness of a food based on the sound it makes while biting into the food versus when actually biting the food itself. Each dot represents a separate food [Source: [70]].

academic and applied food research started to wonder whether the same principles of multisensory integration that had initially been outlined in the anaesthetized animal model might not also be applicable to the multisensory perception of food and beverages in the awake consumer (see [5,74,75], for reviews that capture this burgeoning new approach to the study of flavour). It is to this field of research, sometimes referred to as gastrophysics [8,76,77], that we now turn.

Manipulating mastication sounds

The first research study based on the multisensory approach to flavour perception that involved sound was published in 2004. Zampini and Spence [78] took a crossmodal interaction that had originally been discovered in the psychophysics laboratory—namely, 'the parchment skin illusion'—and applied it to the world of food. In this perceptual illusion, the dryness/texture of a person's hands can be changed simply by changing the sound that they hear when they rub their palms together [79-81]. Max Zampini and I wanted to know whether a similar auditory modulation of tactile perception would also be experienced when people bit into a noisy food product as well.

To this end, a group of participants was given a series of potato chips to evaluate. The participants had to bite each potato chip between their front teeth and rate it in terms of its 'freshness' or 'crispness' using an anchored visual analogue scale displayed on a computer monitor outside the window of the booth. In total, over the course of an hour-long experimental session, the participants bit into 180 Pringles, one after the other. During each trial, the participants received the real-time auditory feedback of the sounds associated with their own biting action over closed-ear headphones. Interestingly though, the participants typically perceived the sound as coming from the potato chip in their mouth, rather than from the headphones, due to the well-known ventriloquism illusion [82][c]. On a crisp-by-crisp basis, this auditory feedback was manipulated by the computer controlling the experiment in terms of its overall loudness and/or frequency composition. Consequently, on some trials, the participants heard the sounds that they were actually making while biting into a crisp. On other trials, the overall volume of their crisp-biting sounds might have been attenuated by either 20 or 40 dB. The higher frequency components of the sound (>2 kHz) could also either be boosted or attenuated (by 12 dB) on some proportion of the trials. Interestingly, on debriefing, three quarters of the participants thought that the crisps had been taken from different packs during the course of the experiment.

The key result to emerge from Zampini and Spence's [78] study was that participants rated the potato chips as tasting both significantly crisper and significantly fresher when the overall sound level was increased and/or when just the high-frequency sounds were boosted (see Figure 2). By contrast, the crisps were rated as both staler and softer when the overall sound intensity was reduced and/or when the high-frequency sounds associated with their biting into the potato chip were attenuated instead.

Recently, a group of Italian scientists has extended this approach to study the role of sound in the perception of the crispness and hardness of apples [83]. Once again, reducing the auditory feedback was shown to lead to a reduction in the perceived crispness of the 'Renetta Canada', 'Golden Delicious', and 'Fuji' apples that were evaluated. More specifically, a small but significant reduction in mean crispness and hardness ratings was observed for this moist food product (contrasting with dry food products such as crisps), when the participants' high-frequency biting sounds were attenuated by 24 dB and/or when there was an absolute reduction in the overall sound level. Thus, it would appear that people's perception of the textural properties of both dry and moist food products can be changed simply by modifying the sounds that we hear[d].

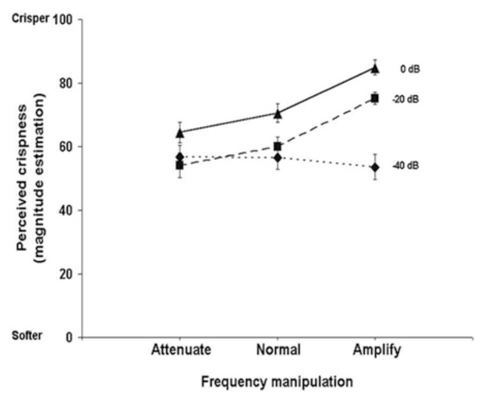

Figure 2 **Results of a study showing that the sound we hear influences the crispness of the crisp [Source: [78]].**

The sound of carbonation

Our perception of the carbonation in a beverage is based partly on the sounds of effervescence and popping that we hear when holding a drink in our hand(s): Make the carbonation sounds louder, or else make the bubbles pop more frequently, and people's judgments of the carbonation of a beverage go up [84]. That said, Zampini and Spence also reported that these crossmodal effects dissipate once their participants took a mouthful of the drink into their mouth. It would appear that the sour-sensing cells that act as the taste sensors for carbonation [85] and/or the associated oral-somatosensory cues [86] likely dominate the overall experience as soon as we take a beverage into our mouths, which, after all, is what we all want to do when we drink[e]. The bottom line here, then, is probably that oral-somatosensory and auditory cues play somewhat different roles in the perception of different food attributes. The research that has been published to date suggests that people appear to rely on their sense of touch more when judging the hardness of foods and the carbonation of drinks in the mouth. By contrast, the two senses (of hearing and oral-somatosensation) would appear to make a much more balanced contribution to our judgments of the crispiness of foods. And crackly may, if anything, be a percept that is a little more auditory dominant than the others.

The sound of creaminess

Not only do different foods make qualitatively different sounds when we bite into or chew them, but our mouth itself sometimes starts to sound a little different as a function of the food that we happen to put into it. This field of research is known as 'acoustic tribology' [87,88]. One simple way to demonstrate this phenomenon is with a cup of strong black coffee. Find a quiet spot and take a mouthful. Swill the coffee around your mouth for a while and then swallow. Now rub your tongue against the top of your mouth (the palate) and think about the feeling you experience and the associated sound that you hear. Next, add some cream to your coffee and repeat the procedure. If you listen carefully enough, you should be able to tell that the sound and feel are quite different the second time around (see [89], for a video). In other words, once the cream has coated your oral cavity, your mouth really does start to make a subtly different sound because of the associated change in friction. Who knows whether our brains use such auditory cues in order to ascertain the texture of that which we have put into our mouths. The important point to note is that these sonic cues are always available, no matter if we pay attention to them or not. And some researchers have argued that such subtle sounds do indeed contribute to our perception of creaminess [90].

Squeaky foods

Now, 'squeaky' probably is not one of the first sounds that comes to mind when contemplating noisy foods. However, we should not neglect to mention this most unusual of sensations. Typically, this descriptor is used when talking about the sound we make when biting into halloumi cheese [91]. It is an example of the stick–slip phenomenon [92]. While the original version comes from Cyprus, the Fins have their very own version called Leipäjuusto [93]. While many people like the sound nowadays [94], traditionally, it was apparently judged to be rather unattractive (see [10], p. 228).

Interim summary

Taken together, the results of the cognitive neuroscience-inspired food research that has been published to date (e.g. [78]) provide support for the claim that modifying food-related auditory cues, no matter whether those sounds happen to come from the food itself (as in the case of a carbonated beverage) or result from a person's interaction with it (as in the case of someone biting into a crisp), can indeed impact on the perception of both food and drink. That said, it should be noted that the products that have been used to date in this kind of research have been specifically chosen because they are inherently noisy. It would seem reasonable to assume that the manipulation of food-related auditory cues will have a much more pronounced effect on the consumer's perception of such noisy foods than that on their impression of quieter (or silent) foodstuffs—think sliced bread, bananas, or fruit juice. Having said that, bear in mind that many foods make some sort of noise when we eat them: Not just crisps and crackers but also breakfast cereals and biscuits, not to mention many fruits and vegetables (think apples, carrots, and celery).[f] Even some seemingly silent foods sometimes make a distinctive sound if you listen carefully enough: Just think, for instance, of the subtle auditory cues that your brain picks up as your dessert spoon cuts through a beautifully prepared mousse. And, as we have just seen, even creaminess makes your mouth sound a little different.

On the commercialization of crunch

Given the above discussion, it should come as little surprise to find that a number of the world's largest food producers (e.g. Kellogg's, Nestlé, Proctor & Gamble, Unilever, etc.) are now starting to utilize the cognitive neuroscience approach to the multisensory design (and modification) of their food products. Kellogg's, for one, certainly believes that the crunchiness of the grain (what the consumer hears and feels in the mouth) is a key driver of the success of their cornflakes (see [95], p. 12). According to Vranica [96]: '*chip-related loudness is viewed as an asset. Frito-Lay has long pitched many of its various snacks as crunchy. Cheetos has used the slogan "The cheese that goes crunch!" A Doritos ad rolled out in 1989 featured Jay Leno revealing the secret ingredient: crunch.*' Once upon a time, Frito-Lay even conducted research to show that Doritos chips give off the loudest crack [97]. This harking back to the 1953 commercial created by the Doyle Dane Bernbach 'Noise Abatement League Pledge' claiming that Scudder's were 'the noisiest chips in the world' (http://www.youtube.com/watch?v=293DQxMh39o; [98]).

In principle, the experimental approach developed by Zampini and Spence [78] enables such companies to evaluate a whole range of novel food or beverage sounds without necessarily having to go through the laborious process of trying to create each and every sound by actually modifying the ingredients or changing the cooking process (only to find that the consumer does not like the end result anyway). Clearly, then, sound is no longer the forgotten flavour sense as far as the big food and drink companies are concerned. Indeed, from my own work with industry, I see a growing number of companies becoming increasingly interested in the sounds that their foods make when eaten.

Of course, sometimes, it turns out to be impossible to generate the food sounds that the consumers in these laboratory studies rate most highly. At least, though, the food manufacturer has a better idea of what it is they are aiming for in terms of any modification of the sound of their product. In a way, the approach to the auditory design of foods is one that the car industry have been utilizing for decades, as they have tried to perfect the sound of the car door as it closes [99] or the distinctive sound of the engine for the driver of a high-end marque (see [35], for a review).

Caveats and limitations

Before moving on, it is important to note that Zampini and Spence [78] did not modify the bone-conducted auditory cues (that are transmitted through the jaw) when their participants bit into the potato chips in their study[g]. Given that we know that such sounds play an important role in the evaluation of certain foodstuffs [59,100], it will certainly be interesting in future research to determine whether there are ways in which they can either be cancelled out, or else modified, while eating (in order to better understand their role in consumer perception). It should also be noted here that Zampini and Spence's auditory feedback manipulations were certainly not subtle [78,84]. A 40-dB difference in sound level between the loudest and quietest auditory feedback conditions is a fairly dramatic change—just remember here that every 10 dB increase in the sound level equates to a doubling of the subjective loudness of a sound. That said, subsequent research has shown that similar crossmodal effects of sound on texture can also be obtained using much more subtle auditory manipulations.

Another important point to bear in mind here is that much of the research demonstrating the influence of auditory cues on texture perception has been based on judgments of the initial bite [78,83]. However, if Harrington and Pearson's [101] early observation that people commonly make between 25 and 47 bites before they end up swallowing a piece of pork meat is anything to go by, then one would certainly want to evaluate judgement of a food's texture after swallowing (rather than after the first bite) in order perhaps to get a better picture of just how important what we hear really is to our everyday eating experiences (see Figure 3). That said, remember here that our first experience of a food very often plays by far the most important role in our experience of, and subsequent memory for, that which we have consumed [102][h]. Indeed, observational studies

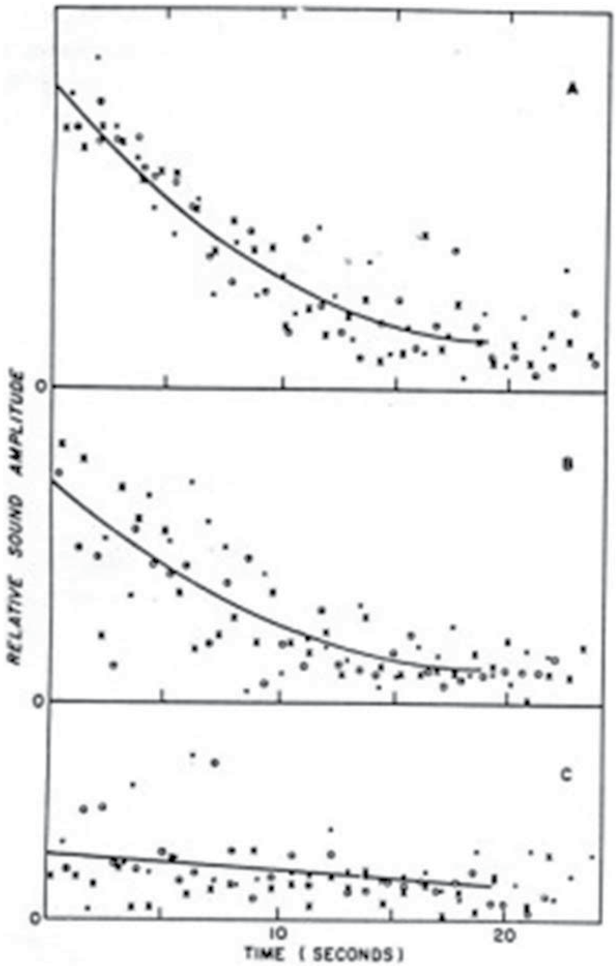

Figure 3 Graphs highlighting the general decline in the amplitude of mastication sounds for (A) crisp brown bread, (B) a half peanut, and (C) an apple as a function of the time spent masticating. The different symbols refer to different experiments conducted with each of the foods [Source: [45]; Figure Ten].

show that people normally use the auditory cues generated during the first bite when trying to assess crispness of a food ([39,103]; see also [70]).

Finally here, it should be noted that the boosting of all sound frequencies above 2 kHz might not necessarily be the most appropriate manipulation of the sound envelope associated with food mastication/consumption sounds. Tracing things back, such broad amplification/attenuation was first introduced by researchers working in the lab on the parchment skin illusion [80]. These sonic manipulations were then adopted without much further modification by food researchers. As it happens, Pringles do tend to make a lot of noise at frequencies of 1.9 kHz and above when crushed mechanically [59,104]. Hence, boosting or attenuating all sounds above 2 kHz will likely have led to a successful manipulation of the relevant auditory cues in the case of Zampini and Spence's [78] Pringles study. I am not aware of any research that has documented the most important auditory characteristics of the sound of the popping of a carbonated drink. In the future, it will be interesting to determine which specific auditory frequency bands convey the most salient information to the consumer when it comes to different classes of products and/or different product attributes (be it crispy, crunchy, crumbly, crackly, creamy, moist, sticky, fizzy, etc.).

Mismatching masticating sounds

On occasion, researchers have investigated the consequences of presenting sounds locked to the movement of a person's jaw that differ from those actually emanating from the mouth. There are, for instance, anecdotal reports of Jon Prinz having his participants repeatedly chew on a food in time with a metronome. After a few ticks, Prinz would take his subject by surprise and suddenly play the sound of breaking glass (or something equally unpleasant) just as they started to bite down on the food! Apparently, his subjects' jaws would simply freeze-up. It was almost as if some primitive self-preservation reflex designed to avoid bodily harm had suddenly taken over.

Meanwhile, Japanese researchers pre-recorded the sound of their participants masticating rice crackers (a food that has a particularly crunchy texture) and rice dumplings (which, by contrast, have a very sticky texture; [105]). These sounds were then played back over headphones while participants chewed on a variety of foods including fish cakes, gummy candy, chocolate pie, marshmallow, pickled radish, sponge cake, and caramel corn. Importantly, the onset of the mastication sounds was synchronized with those of the participant's own jaw movements. The ten people who took part in this study had to estimate the degree of texture change and the pleasantness of the ensuing experience either with or without added mastication sounds. Crucially, regardless of the particular food being tested (or should that be tasted), the perceived hardness/softness, moistness/dryness, and pleasantness of the experience were all modified by the addition of sound. Specifically, the foods were rated as harder and dryer when the rice cracker sounds were presented than without any sonic modification. By contrast, adding the sound of masticating dumplings resulted in the foods' texture being rated as softer and moister than under normal auditory feedback.

Finally, the participants in another study from the same research group were given two chocolates that had a similar taste but a very different texture: one called Crunky (Lotte) was a crunchy chocolate that contained malt-puffs and hence gave rise to loud mastication sounds. The other, Aero (Nestle), contains nothing but air bubbles and hence does not make too much noise at all when eaten. The pre-recorded mastication sounds of the crunchy chocolate were then presented while the blindfolded participants chewed on a piece of the other chocolate.[i] The participants bit into both kinds of chocolate while either listening only to their self-generated mastication sounds, or else while the pre-recorded crunchy sounds were played back over noise cancelling headphones [106]. Interestingly, the Aero chocolate was misidentified as the Crunky chocolate 10–15% more often when the time-locked crunchy mastication sounds were presented. That said, given that only three participants took part in this study, the findings should not be treated as anything more than preliminary at this stage.

Interim summary

Taken together, the evidence that has been published over the last decade or so clearly highlights the influence that auditory cues have on the oral-somatosensory and textural qualities of a number of different foods. Boosting or attenuating the actual sounds of food consumption or the substituting of another sound that just so happens to be time locked to a person's own jaw movements can nevertheless result in some really quite profound perceptual changes. It seems plausible to look for an explanation of these findings in terms of the well-established principles of multisensory integration [23,72]. Indeed, it would not be at all surprising to find that such crossmodal effects can be effectively modelled in terms of the currently popular 'maximum likelihood estimation' approach to cue integration [107-109]. The basic idea here is that the more reliable a sensory cue is, the more heavily it will be weighted by the brain in terms of the overall multisensory percept than other less reliable cues (e.g. when trying to judge how crispy that crisp really is; see also [110]).

Alternatively, however, it is also worth noting that auditory cues may influence our judgments of food texture because they simply capture our attention much more effectively than do oral-somatosensory cues [111].[j] Indeed, after they had finished the experiment, the majority of Zampini and Spence's [78] participants reported anecdotally that the auditory information had been more salient to them than the oral-tactile cues. Of course, the within-participants design of their study meant that the participants would have been acutely aware of the sound changing from trial to trial, likely accentuated any auditory attentional capture effects.

In the future, it will be interesting to assess the relative contribution, and possible dominance, of certain sensory cues when they are put into conflict/competition with one another in the evaluation and consumption of realistic food products (e.g. see [112,113], for examples along these lines). When the differences between the estimates provided by each of our senses are small, one normally sees integration/assimilation (depending on whether the cues are presented simultaneously or successively). However, when the discrepancy between the estimates provided by the senses differ by too great a margin, then you are likely to see a negatively valenced disconfirmation of expectation response instead [114,115]. That said, if you get the timing right [106], the brain has a strong bias toward combining those cues that are perceived to have occurred at the same time, or that appear to be correlated temporally [116], even if those cues have little to do with one another [117].

Conclusions

Sound is undoubtedly the forgotten flavour sense. Most researchers, when they think about flavour, fail to give due consideration to the sound that a food makes when they bite into and chew it. However, as we have seen throughout this article, what we hear while eating plays an important role in our perception of the textural properties of food, not to mention our overall enjoyment of the multisensory experience of food and drink. As Zata Vickers ([54], p. 95) put it: '*Like flavors and textures, sometimes sounds can be desirable, sometimes undesirable. Always they add complexity and interest to our eating experience and, therefore, make an important contribution to food quality.*' Indeed, the sounds that are generated while biting into or chewing food provide a rich source of information about the textural properties of that which is being consumed, everything from the crunch of the crisp and the crispy sound of lettuce, through to the crackle of your crackling and the carbonation in your cava. Remember also that, evolutionarily speaking, a food's texture would have provided our ancestors with a highly salient cue to freshness of whatever they were eating.

In recent years, many chefs, marketers, and global food companies have started to become increasingly interested in trying to perfect the sound that their foods make, both when we eat them, but also when we see the model biting into our favourite brands on the screen. It is, after all, all part of the multisensory flavour experience. In the future, my guess is that various technologies, some of which will be embedded in digital artefacts, will increasingly come to augment the natural sounds of our foods at the dining table [8,23]. And that is not all. Given the growing ageing population, there may also be grounds for increasing the crunch in our food in order to make it more interesting (not to say enjoyable) for those who are starting to lose their ability to smell and taste food [118]. Finally, before closing, it is worth noting that the majority of the research that has been reviewed in this article has focused on the moment of tasting or consumption. However, on reflection, it soon becomes clear that much of our enjoyment of food and drink actually resides in the anticipation of consumption and the subsequent memories we have, at least when it comes to those food experiences that are worth remembering (see Figure 4). As such, it will undoubtedly be worthwhile for future research to broaden out the timeframe over which our food experiences are studied. As always, then, much research remains to be conducted.

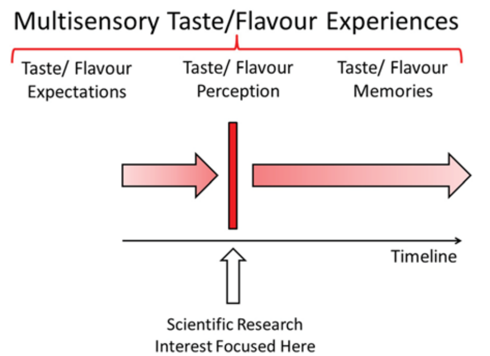

Figure 4 The majority of research on multisensory flavour perception has focused on the moment of consumption. It is, however, important to note that our enjoyment of eating and drinking often extends over a much longer time period, encompassing both the anticipation of consumption and the subsequent memories associated with consumption. Future research will therefore need to start investigating the role of the various senses (and this includes audition) in the broader range of our food-related thoughts and memories.

Endnotes

[a]If you take away the textural cues by pureeing foods, then people's ability to identify them declines dramatically ([12], p. 91).

[b]'Crujiente' = crispy, while crocante comes from the French and has apparently almost disappeared from the Spanish language [63].

[c]This is an audiotactile version of the phenomenon that we all experience when our brain glues the voice we hear onto the lips we see on the cinema screen despite the fact that the sounds actually originate from elsewhere in the auditorium [107].

[d]Of course, at this point, it could be argued that while these studies show that sound plays an important role in the perception of food *texture*, this is not the same as showing an effect on the *flavour* of food itself.

[e]Evolutionarily speaking, carbonation would have served as a signal to our ancestors that a food had gone off, i.e. that a piece of fruit was overripe/fermenting [85], thus making it so surprising that it should nowadays be such a popular sensory attribute in beverages; by contrast, it has been argued that crunchiness is a positive attribute since it signals the likely edibility of a given foodstuff and is associated with freshness [119,120]. It is intriguing to consider here whether this difference in the meaning of different auditory cues (signalling bad vs. good foods, respectively) might not, then, have led to the different results reported here (cf. [121]). On the other hand, though, it also has to be acknowledged that the specific frequency manipulation introduced by Zampini and Spence [78] may simply not have been altogether ecologically valid, or meaningful, in terms of the perception of carbonation [84].

[f]And as we saw earlier, research from Vickers [41,122] has shown that we can use those food biting and mastication sounds in order to identify a food, even when it is someone else who happens to be doing the eating.

[g]Here, we need to distinguish between air-conducted sound, the normal way we hear sound, and bone-conducted sound. It turns out that the jawbone and skull have a maximum resonance at around 160 Hz [33,123].

[h]The pitch of eating sounds changes (specifically it is lowered) by changing from biting to chewing, and, as a result, judgments of crispness tend to be lower ([55,58]; though see [124]). Chew a food with the molars and the mouth closed and what you will hear is mostly the bone-conducted sound, thus lower in pitch.

[i]One might worry here about the effect of blindfolding on participants' judgments [125,126]. However, to date, researchers have been unable to demonstrate a significant effect of blindfolding on people's loudness, pitch, or duration judgments when it comes to their evaluation of food-eating sounds [112].

[j]Rietz [127] would seem to have been thinking of something of the sort when he suggested many years ago that eating blanched almonds with smoked finnan haddie reduced the fishy flavour of the latter through '*an illusion caused by the dominance of the auditory sense over that of taste and smell generated by the kinesthesis of munching*'. However, no experimental evidence was cited in support of this claim.

Competing interests
The author declares that he has no competing interests.

Authors' contributions
CS wrote all the parts of this review. The author read and approved the final manuscript.

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RESEARCH Open Access

Flavour improvement of reduced-fat peanut butter by addition of a *kokumi* peptide, γ-glutamyl-valyl-glycine

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Abstract

Background: Recent studies have demonstrated that *kokumi* substances, which enhance basic tastes and modify mouthfulness and continuity although they have no taste themselves, are perceived through the calcium-sensing receptor (CaSR). Screening by a CaSR assay and sensory evaluation have shown that γ-glutamyl-valyl-glycine (γ-Glu-Val-Gly) is a potent *kokumi* peptide. In our previous study, it was reported that the addition of γ-Glu-Val-Gly to chicken consommé significantly enhanced mouthfulness, continuity and thickness. In this study, the effect of γ-Glu-Val-Gly on reduced-fat peanut butter was investigated.

Results: Prior to the evaluation of the effect of γ-Glu-Val-Gly, a comparison test was conducted between full-fat model peanut butter and reduced-fat peanut butter. The sensory attributes in which the score of the full-fat model was significantly higher than that of the reduced-fat sample were used for the evaluation of the effect of γ-Glu-Val-Gly. The addition of γ-Glu-Val-Gly significantly enhanced thick flavour, aftertaste, and oiliness in the reduced-fat peanut butter.

Conclusions: A *kokumi* peptide, γ-Glu-Val-Gly, can enhance thick flavour, aftertaste and oiliness in reduced-fat peanut butter. This suggests that addition of γ-Glu-Val-Gly can improve the flavour of low-fat foods.

Keywords: Low-fat foods, Reduced-fat foods, Peanut butter, *Kokumi*, γ-glutamyl-valyl-glycine, Sensory evaluation

Background

Recent studies have revealed that *kokumi* substances such as glutathione (GSH) are perceived through the calcium-sensing receptors (CaSRs) in humans [1]. These studies have confirmed that GSH can activate human CaSRs, as can several γ-glutamyl peptides, including γ-Glu-Ala, γ-Glu-Val, γ-Glu-Cys, γ-Glu-α-aminobutyryl-Gly (ophthalmic acid) and γ-Glu-Val-Gly. Furthermore, these compounds have been shown to possess the characteristics of *kokumi* substances, which modify the five basic tastes (especially sweet, salty and umami) when added to basic taste solutions or food, even though they have no taste themselves at the concentrations tested [2-8]. The CaSR activity of these γ-glutamyl peptides is positively correlated with the sensory activity of *kokumi* substances, suggesting they are perceived through the CaSRs in humans. Among these, γ-Glu-Val-Gly has been reported to be a potent *kokumi* peptide with a sensory activity 12.8-fold greater than that of GSH [3].

In our previous study, the effect of γ-Glu-Val-Gly on the sensory characteristics of chicken consommé was investigated. Adding γ-Glu-Val-Gly to chicken consommé significantly enhanced thickness (taste enhancement ~5 s after tasting), continuity (taste intensity at 20 s after tasting), and mouthfulness (the reinforcement of taste sensation throughout the mouth and not just on the tongue) [3]. It is generally known that these sensations are evoked by the addition of fat-containing food materials such as dairy fat emulsion [9].

The problem of the increase in the obese population has resulted in various kinds of reduced-fat foods being developed and commercialised. However, in general, the palatability of reduced-fat foods is lower than that of full-fat foods. In previous studies, it has been demonstrated that the reduced-fat samples have decreased juiciness, greasiness, aftertaste, and overall flavour intensity in

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sausages [10] and decrease the score of creaminess in yogurt [11]. In addition, it has been demonstrated that the reduced-fat samples have lower scores in thickness, smoothness, creaminess, mouth coating and milky/cooked sugar flavour in ice cream [12] and have lower scores in milk fat flavour and brothy flavour in cheddar cheese [13]. To overcome these problems, because reduced-fat foods mainly lack texture, the use of thickeners such as gums, starch and modified starch has been proposed. However, the reduced-fat foods with such additives still have lower palatability than full-fat foods.

In the present study, we aimed to clarify whether addition of γ-Glu-Val-Gly changed the flavour by palatability of reduced-fat foods. We investigated the effect of γ-Glu-Val-Gly on reduced-fat peanut butter.

Results and discussion

In this study, first, the sensory attributes of peanut butter were discussed and selected by expert panellists. Then, panellists rated the differences between reduced- and full-fat peanut butter to establish how increased fat affected the sensory attributes of peanut butter. Finally, the same evaluation was conducted comparing reduced-fat peanut butter and that with *kokumi* peptide, γ-Glu-Val-Gly.

Sensory attributes

During the group discussion, panellists listed up the words, selected the attributes and made a consensus of the sensation which the attribute expressed. Finally, the panellists developed ten attributes: peanut flavour, saltiness, sweetness, bitterness, thick flavour (thickness of taste; the enhancement of taste intensity with maintaining the balance of taste), aftertaste (the total aftertaste intensity after 5 s of all flavour notes within the sample), continuity of taste (the taste intensity at ~20 s), smoothness, and oiliness.

Comparison between reduced-fat sample and full-fat model of peanut butter

Comparison between reduced-fat peanut butter and full-fat model peanut butter is shown in Table 1. The full-fat model peanut butter had higher scores for peanut flavour, thick flavour, aftertaste, continuity of taste, and oiliness than for low-fat peanut butter. No significant difference in saltiness, sweetness, bitterness, smoothness, and viscous sensation was observed between the low-fat sample and full-fat model. We consider that the fat enhanced the above sensory character in peanut butter. In other words, we considered that peanut flavour, thick flavour, aftertaste, continuity of taste, and oiliness were the sensory functions of fat in peanut butter.

Table 1 Result of the comparison test between low-fat peanut butter and full-fat model peanut butter

Sensory attributes	Score of full-fat model	Significance
Peanut flavour	0.24 ± 0.05	**
Saltiness	0.04 ± 0.04	NS
Sweetness	−0.03 ± 0.05	NS
Bitterness	−0.10 ± 0.05	NS
Thick flavour	0.15 ± 0.06	*
Aftertaste	0.16 ± 0.04	**
Continuity of taste	0.14 ± 0.04	**
Smoothiness	0.10 ± 0.08	NS
Viscosity	−0.01 ± 0.09	NS
Oiliness	0.23 ± 0.07	**

Description of data: data was shown as means ± standard errors.
Abbreviation: *NS* not significant.
*$p < 0.05$; **$p < 0.01$.

Effect of addition of γ-Glu-Val-Gly in reduced-fat peanut butter

To clarify the effect of γ-Glu-Val-Gly on the sensory character of reduced-fat peanut butter, reduced-fat peanut butter with 40 ppm γ-Glu-Val-Gly was evaluated for the attributes, peanut flavour, thick flavour, aftertaste, continuity of taste, and oiliness. The results of the sensory evaluation are shown in Table 2. Addition of γ-Glu-Val-Gly significantly enhanced the intensities of thick flavour, aftertaste, and oiliness. These results demonstrated that the addition of γ-Glu-Val-Gly increased some sensations that were lacking in the reduced-fat peanut butter, suggesting that addition of the peptide can be used for flavour improvement in reduced-fat peanut butter.

The previous studies described that the several reduced-fat foods and low-fat foods lacked the sensations related to ‘thick flavour’, ‘aftertaste’ and ‘oiliness’. For example, it has been previously reported that the low-fat sausage has lower juiciness and aftertaste intensity [10] and that low-fat yogurt has lower creaminess [11] than full-fat products. In addition, it has been previously reported that reduced-fat ice cream indicated lower scores of texture-related attributes such as thickness, smoothness, creaminess,

Table 2 Effect of γ-Glu-Val-Gly on the low-fat peanut butter

Sensory attributes	Score of sample with γ-Glu-Val-Gly	Significance
Peanut flavour	0.06 ± 0.05	NS
Thick flavour	0.13 ± 0.04	**
Aftertaste	0.14 ± 0.05	*
Continuity of taste	0.09 ± 0.05	NS
Oiliness	0.09 ± 0.04	*

Data was shown as means ± standard errors.
Abbreviation: *NS* not significant.
*$p < 0.05$; **$p < 0.01$.

mouth coating than those of full-fat products [12]. Therefore, it is considered that the addition of γ-Glu-Val-Gly can be used to improve the flavour of other reduced-fat foods. In order to clarify this possibility, it is necessary to conduct a preference test using a consumer panel, and this test is now in progress in our laboratory. The effect of γ-Glu-Val-Gly on other reduced-fat foods is also now under investigation in our laboratory.

Conclusions

In this study, the effect of a *kokumi* peptide, γ-Glu-Val-Gly, on the flavour of reduced-fat peanut butter was investigated. The results indicated that the addition of γ-Glu-Val-Gly significantly enhanced the intensities of thick flavour, aftertaste, and oiliness. These results demonstrated that addition of γ-Glu-Val-Gly increased some sensations that were lacking in the reduced-fat peanut butter, suggesting that addition of the peptide could improve the flavour of reduced-fat peanut butter.

Methods

Preparation of γ-Glu-Val-Gly

The γ-Glu-Val-Gly used in the present study was of food additive grade (FEMA-GRAS No. 4709; Flavor and Extract Manufacturers Association (FEMA); JECFA food flavouring No. 2123; Joint FAO/WHAO Expert Committee on Food Additives (JECFA)) obtained from Ajinomoto Co. Inc. (Tokyo, Japan) and was prepared by chemical synthesis as reported previously [1].

Preparation of reduced-fat peanut butter and full-fat peanut butter model

The raw materials for reduced-fat peanut butter (30% fat content) and full-fat peanut butter model (50% fat content) are shown in Table 3. Regarding the preparation of the reduced-fat peanut butter, the emulsifiers were mixed with peanut paste in an aluminium pot at 30°C with later addition of cream by stirring. Sugar and salt solubilised in water were added, stirred, and heated at 40°C for 5 min. Regarding the preparation of the full-fat model peanut butter, the emulsifiers were mixed with peanut paste and salad oil in an aluminium pot at 30°C with later addition of cream by stirring. Sugar and salt solubilised in water were added, stirred, and heated at 40°C for 5 min. As for the reduced-fat peanut butter with γ-Glu-Val-Gly, γ-Glu-Val-Gly was added by dissolving in water with sugar and salt. Prepared peanut butter samples were packed in glass bottles and stored at 4°C until sensory evaluation.

Table 3 Raw materials for the low-fat peanut butter and full-fat model peanut butter

Materials	Low-fat (wt.%)	Full-fat model (wt.%)
Peanut paste	55.0	55.0
Salad oil	0.0	21.0
Salt	1.0	1.0
Sugar (granulated)	6.2	6.2
Cream	5.0	5.0
Emulsifier (sugar-ester; HLB:15)	2.0	0.5
Emulsifier (glyceryl monostearate; HLB:4)	0.0	2.0
Xantan gum	0.0	0.5
Water	30.8	8.8

Selection of the sensory panel

In this study, 29 panellists (17 men and 12 women; 28.8 ± 5.0 years old, mean ± standard deviation) participated in the sensory evaluation. All panellists were the employees of Ajinomoto Shanghai Food Research and Technology Center and were working on the development of foods. They were Chinese and were residents of Shanghai city. In addition, all of them passed the sensory panel examination conducted using a previously described method [14]. For the comparison between the reduced-fat peanut butter and full-fat model, 20 panellists (9 men and 11 women; 27.6 ± 3.6 years old, mean ± standard deviation) participated in the sensory evaluation. For the investigation of the effect of γ-Glu-Val-Gly, 19 panellists (13 men and 6 women; 29.9 ± 5.3 years old, mean ± standard deviation) participated in the evaluation.

Selection of the sensory attributes

Panellists evaluated samples of the reduced-fat peanut butter and full-fat peanut butter model. A panel leader led the group in discussion on the differences and similarities between the samples. They developed a list of sensory attributes that described the sensory characteristics of the products. The panellists developed ten attributes: peanut flavour, saltiness, sweetness, bitterness, thick flavour, aftertaste, continuity of taste, smoothness, viscosity and oiliness. The panellists practiced rating the samples on the list so that they were prepared to begin data collection.

Procedure for sensory evaluation

The sensory evaluation was conducted between 10:00 am and 11:30 am in the partitioned booth at 25°C in an air-conditioned sensory evaluation room. For evaluation of the peanut butter samples, 10 g of the sample was spread on one piece of bread (10 g), which was cut into four pieces. The panellists held each piece of bread with peanut butter in the mouth, evaluated the taste, and rated each attribute. They rinsed their mouths with commercial mineral water between the samples. They completed the rating for each attribute on a three-point linear scale; −1.0: apparently weaker than the control; 0: same as the control; and 1.0: apparently stronger than the control. For comparison between the reduced-fat sample and full-fat model, half of the panellists evaluated the full-fat model using a reduced-fat sample as the control and the other half evaluated the reduced-fat sample using a full-fat model as the control. Combination of the samples was randomised and balanced. Human sensory analyses were conducted following the spirit of the Helsinki Declaration, and informed consent was obtained from all panellists. The experimental procedure was approved by the Ethics Board of the Institute of Food Sciences and Technologies, Ajinomoto.

Statistical analysis

Statistical analysis was conducted using JMP version 9.0 (SAS Institute, Cary, NC, USA). The data were collected as the means ± standard error. Data were assessed by the paired *t*-test. The data were considered to be significant at $p < 0.05$.

Abbreviations

γ-Glu-Val-Gly: γ-Glutamyl-valyl-glycine; GSH: glutathione; CaSR: calcium-sensing receptor; FEMA: Flavour and Extract Manufacturers Association; JECFA: The Joint FAO/WHO Expert Committee.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MK, NH and TK conceived this study. SJ and NM designed the detail of experiments. SJ conducted sample preparation and sensory evaluation. SJ and MK conducted sensory data analysis, and MK wrote the manuscript. All authors read and approved the final manuscript.

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RESEARCH Open Access

Effect of a *kokumi* peptide, γ-glutamyl-valyl-glycine, on the sensory characteristics of chicken consommé

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Abstract

Background: Recent studies have demonstrated that *kokumi* substances such as glutathione are perceived through the calcium-sensing receptor (CaSR). Screening by a CaSR assay and sensory evaluation have shown that γ-glutamyl-valyl-glycine (γ-Glu-Val-Gly) is a potent *kokumi* peptide. In the present study, the sensory characteristics of chicken consommé with added γ-Glu-Val-Gly were investigated using descriptive analysis.

Results: Chicken consommé containing γ-Glu-Val-Gly had significantly stronger "umami" and "mouthfulness" (mouth-filling sensation) characteristics than the control sample at a 99% confidence level and significantly stronger "mouth-coating" characteristic than controls at a 95% confidence level.

Conclusions: These data suggest that a *kokumi* peptide, γ-Glu-Val-Gly, can enhance umami, mouthfulness, and mouth coating, implying that the application of this peptide could contribute to improving the flavor of chicken consommé.

Keywords: Chicken consommé, Kokumi, γ-Glutamyl-valyl-glycine, γ-Glu-Val-Gly, Sensory evaluation, Descriptive analysis

Background

Taste and aroma are important factors in determining the flavor of foods. Sweet, salty, sour, bitter, and umami comprise the five basic tastes with each taste being recognized by specific receptors and associated with particular transduction pathways. However, foods have sensory attributes that cannot be explained by aroma and the five basic tastes alone: texture, continuity, complexity, and mouthfulness. Ueda et al. investigated the flavoring effects of a diluted extract of garlic that enhanced continuity, mouthfulness, and thickness when added to an umami solution and attempted to isolate and identify the key compounds responsible for this effect [1]. Their study indicated that sulfur-containing compounds such as S-allyl-cysteine sulfoxide (alliin), S-methyl-cysteine sulfoxide, γ-glutamyl-allyl-cysteine, and glutathione (γ-glutamyl-cysteinyl-glycine; GSH) led to this flavoring effect. These compounds have only a minimal flavor in water, but if added to an umami solution or other types of food, they can substantially enhance the thickness, continuity, and mouthfulness of the food to which they have been added [2]. They proposed that substances with these properties should be referred to as *kokumi* substances.

Recently, it was reported that *kokumi* substances such as GSH are perceived through the calcium-sensing receptor (CaSR) in humans [3]. These studies confirmed that GSH can activate human CaSR, as can several γ-glutamyl peptides, including γ-Glu-Ala, γ-Glu-Val, γ-Glu-Cys, γ-Glu-α-aminobutyryl-Gly (ophthalmic acid), and γ-Glu-Val-Gly. Furthermore, these compounds have been shown to possess the characteristics of *kokumi* substances, which modify the five basic tastes (especially sweet, salty, and umami) when added to basic taste solutions or food, even though they have no taste themselves at the concentrations tested [1,2,4-8]. The CaSR activity of these γ-glutamyl peptides has also been shown to be positively correlated with the sensory activity of *kokumi* substances, suggesting they are perceived through the CaSR in humans. Among these, γ-Glu-Val-Gly has been reported to be a potent *kokumi* peptide with a sensory activity 12.8-fold times greater than that of GSH [3]. Additionally, it has been reported that γ-Glu-Val-Gly

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was present in several foods such as scallops [9], fermented fish sauces [10], soy sauces [11], and fermented shrimp pastes [12]. Ohsu et al. also reported that adding 0.01% γ-Glu-Val-Gly to 3.3% sucrose solution, 0.9% NaCl solution, and 0.5% monosodium glutamate (MSG) solution significantly enhanced sweetness, saltiness, and umami, respectively [3]. They also reported that adding 0.002% γ-Glu-Val-Gly to chicken consommé prepared from commercial chicken consommé powder significantly enhanced thickness, continuity, and mouthfulness. In that report, sensory evaluation was undertaken with sensory attributes with reference to a method reported previously [1,2]. The sensory attributes used in these previous research works such as thickness, mouthfulness, and continuity were originally extracted using the sensory evaluation which compared the sensory profiles of various foods, mainly soups, with and without MSG [13]. Therefore, to clarify the sensory characteristics of food with added γ-Glu-Val-Gly, a more detailed study comparing the sensory attributes of food with and without this peptide has been needed.

In the present study, we aim to characterize the sensory properties of food with added γ-Glu-Val-Gly, through performing a descriptive analysis of chicken consommé containing the peptide.

Results and discussion

Sensory attributes for chicken consommé

During the project-specific orientation session, the panelists developed 17 attributes shown in Table 1. Regarding the attributes related to chicken flavor, since many words related to the chicken flavor were proposed during the project-specific orientation session, three attributes “total chicken/meaty flavour”, “bones/marrow flavour”, and “roasted flavour” were added to the list. Total chicken/meaty flavor was defined as the flavor intensity reminiscent of cooked chicken meat; bones/marrow flavor was defined as the character associated with chicken bones, particularly the marrow of chicken bones; and roasted flavor was defined as the total flavor intensity that is reminiscent of roasted chicken and/or vegetables. Additionally, because the coating sensation was well recognized when the panelists evaluated the chicken consommé with γ-Glu-Val-Gly during the project-specific panel orientation session, the attributes “mouth-coating” and “tongue-coating” were added to the list. “Mouth-coating” was defined as the degree to which there is a leftover residue, a slick, powdery, or fatty coating or film on the mouth that is difficult to clear. “Tongue-coating” was defined as the degree to which there is a leftover residue, a slick, powdery, or fatty coating or film on the tongue that is difficult to clear. Overall, the panelists defined the 17 sensory attributes for chicken consommé listed in Table 1: nine taste and flavor attributes (total flavor, total chicken/meaty flavor, chicken flavor, bones/marrow, roasted flavor, total vegetable flavor, richness, salty, and umami), seven texture/mouthfeel attributes (viscosity, mouthfulness, mouth coating, tongue coating, salivating, total trigeminal, and swelling perception of soft tissue), and one aftertaste (total aftertaste). The definitions of these sensory attributes and the references are shown in Table 2.

Sensory characteristics of chicken consommé with added γ-Glu-Val-Gly

The sensory characteristics of chicken consommé with or without γ-Glu-Val-Gly are shown in Table 2 and Figure 1. The addition of γ-Glu-Val-Gly at 5 ppm significantly enhanced the intensity of umami and mouthfulness at a 99% confidence level. Furthermore, the addition of this peptide significantly enhanced the intensity of mouth coating at a 95% confidence level. Adding this peptide at 5 ppm did not significantly change the intensity of the other attributes. A recent study has suggested that *kokumi* peptides such as GSH and γ-Glu-Val-Gly enhance the intensity of umami if they are added to 0.5% MSG solution [3], an observation consistent with the present study. Additionally, in the descriptive analysis, umami has been defined not only as the “taste of MSG” but also as “the mouth-filling sensation of compounds such as glutamates that is savoury, brothy, meaty, rich, full, and complex, which is common to many foods such as soy sauce, stocks, ripened cheese, shellfish, mushrooms, ripened tomatoes, cashews, and asparagus”. Therefore, it appears that the enhancement of umami in chicken consommé includes the enhancement of sensations such as richness and complexity. The present results also suggest that γ-Glu-Val-Gly also enhanced mouthfulness. A previous study demonstrated that adding γ-Glu-Val-Gly at 20 ppm to chicken soup significantly enhanced mouthfulness which is consistent with the present study [3]. Regarding other γ-glutamyl peptides, it has been reported that several *kokumi* γ-glutamyl peptides enhanced mouthfulness in food systems. Ueda et al. reported that the addition of GSH (γ-Glu-Cys-Gly) enhanced the intensity of mouthfulness in model beef meat extract [2]. In addition, Ohsu et al. also reported that the addition of GSH enhanced the intensity of mouthfulness in chicken soup [3]. Furthermore, it has been reported that γ-glutamyl peptides such as γ-Glu-Val, γ-Glu-Leu, and γ-Glu-Cys-βAla found as *kokumi*-active peptides in edible beans enhanced mouthfulness when they were added to chicken broth [5]. In addition, it has been reported that γ-Glu-Glu, γ-Glu-Gly, γ-Glu-His, γ-Glu-Gln, γ-Glu-Met, and γ-Glu-Leu were the key components which impart long-lasting mouthfulness of matured Gouda cheese. From these observations, it is demonstrated that many *kokumi* γ-glutamyl peptides enhance the intensity of mouthfulness.

Table 1 Definition and reference samples for the descriptive attributes of chicken consommé

Sensory attributes	Definitions	Reference samples and intensity
Total flavor	The total intensity of all of the flavors of the sample including basic tastes	Kitchen Basics chicken broth (6)
Total chicken/meaty flavor	The flavor intensity reminiscent of cooked chicken meat	Kitchen Basics chicken broth (5)
Chicken flavor	The flavor intensity reminiscent of cooked chicken	Kitchen Basics chicken broth (5)
Bones/marrow flavor	The character associated with chicken bones, particularly the marrow of chicken bones	NR
Roasted flavor	The total flavor intensity that is reminiscent of roasted chicken and/or vegetables	Swanson's chicken broth (6)
Total vegetable flavor	The total flavor intensity of vegetables such as carrots, green vegetables, and herbs in the broth	Kitchen Basics chicken broth (5)
Richness	The degree to which the flavor characters of the sample are harmonized, balanced, and blend well together as opposed to being spiky or striking out	NR
Salty	One of the basic taste, common to sodium chloride	0.2% sodium chloride in water (2) 0.5% sodium chloride in water (5) 0.2% sodium chloride in water (2) 0.5% sodium chloride in water (5)
Umami	One of the basic taste, common to MSG. The taste and mouth-filling sensation of compounds such as glutamates that is savory, brothy, meaty, rich, full, and complex, common to many foods such as soy sauce, stocks, ripened cheese (especially parmesan), shellfish (crab, lobster, scallops, clams), mushrooms (especially porcini), ripe tomatoes, cashews, and asparagus	Kitchen Basics chicken broth (2) 0.5% MSG in Kitchen Basics chicken broth (3.5) Kitchen Basics chicken broth (2) 0.5% MSG in Kitchen Basics chicken broth (3.5)
Viscosity	The degree to which the samples are viscous in the mouth from thin to thick	Water (1) Heavy whipping cream (6)
Mouthfulness	The perception that the sample fills the whole mouth is blooming, or growing, a full-bodied sensation when the sample is held in the mouth	Kitchen Basics chicken broth (1.5) 0.5% MSG in Kitchen Basics chicken broth (3) Kitchen Basics chicken broth (1.5) 0.5% MSG in Kitchen Basics chicken broth (3)
Mouth coating	The degree to which there is a leftover residue, a slick, powdery, or fatty coating or film in the mouth that is difficult to clear	0.5% MSG in water (4) Half and Half (5) 0.5% MSG in water (4) Half and Half (5)
Tongue coating	The degree to which there is a leftover residue, a slick, powdery, or fatty coating or film on the tongue that is difficult to clear	0.5% MSG in water (3)
Total trigeminal	The intensity of the total sensation, including numbing, burning, tingling, or irritation, impaired on the soft tissues of the oral cavity, particularly the tongue	Wintergreen breathsaver (NS) 0.5% MSG in water (5) Wintergreen breathsaver (NS) 0.5% MSG in water (5)
Salivating	The degree to which the sample caused a perceived increase in salivation	NR
Swelling of cheeks and lips	The feeling of swelling of the soft tissue in the oral cavity, specifically the cheeks and lips, reminiscent of the perception of swelling produced by antithetic treatments at a dental office, but without a distinct numbing effect	0.5% MSG in water (4)
Total aftertaste	The total aftertaste intensity after 5 s of all flavor notes within the sample	NR

NR no reference, *NS* not scored.

Table 2 Sensory characteristics of chicken consommé with added γ-Glu-Val-Gly

Sensory attributes	Control consomme	Consomme with γ-Glu-Val-Gly	Changed value	95% confidence interval	99% confidence interval	Significance
Total flavor	6.13 ± 0.72	6.31 ± 0.68	0.18 ± 0.60	0.28	0.36	N.S.
Total chicken/meaty flavor	5.26 ± 0.61	5.41 ± 0.59	0.14 ± 0.59	0.27	0.36	N.S.
Chicken flavor	4.82 ± 0.55	4.88 ± 0.78	0.06 ± 0.69	0.32	0.42	N.S.
Bones/marrow flavor	2.42 ± 0.85	2.63 ± 0.98	0.21 ± 1.14	0.53	0.69	N.S.
Roasted flavor	3.19 ± 1.03	3.12 ± 1.03	−0.07 ± 0.82	0.38	0.50	N.S.
Total vegetable flavor	3.56 ± 0.75	3.78 ± 0.81	0.22 ± 0.64	0.30	0.39	N.S.
Richness	4.01 ± 0.81	4.27 ± 0.94	0.27 ± 0.79	0.36	0.48	N.S.
Salty	2.73 ± 0.48	2.87 ± 0.73	0.13 ± 0.57	0.26	0.35	N.S.
Umami	2.84 ± 0.65	3.28 ± 0.67	0.43 ± 0.66	0.30	0.40	**
Viscosity	2.06 ± 0.65	2.22 ± 0.59	0.16 ± 0.40	0.18	0.24	N.S.
Mouthfulness	2.47 ± 0.70	2.92 ± 0.73	0.45 ± 0.69	0.32	0.42	**
Mouth coating	2.67 ± 0.66	2.94 ± 0.65	0.27 ± 0.56	0.26	0.34	*
Tongue coating	2.56 ± 0.82	2.72 ± 0.82	0.17 ± 0.68	0.32	0.42	N.S.
Salivating	2.42 ± 0.85	2.58 ± 0.83	0.16 ± 1.06	0.49	0.64	N.S.
Total trigeminal	2.76 ± 0.87	2.98 ± 0.73	0.23 ± 0.84	0.39	0.51	N.S.
Swelling perception of soft tissue	2.78 ± 0.79	2.87 ± 0.68	0.09 ± 0.76	1.48	0.46	N.S.
Total aftertaste	4.46 ± 0.60	4.54 ± 0.66	0.08 ± 0.64	0.29	0.38	N.S.

Data was shown as means ± standard errors.
N.S. not significant.
*Significant at a 95% confidence level, **significant at a 99% confidence level.

Interestingly, the present study has revealed that the addition of γ-Glu-Val-Gly at 5 ppm significantly enhanced the intensity of mouth coating. It has been generally known that mouth-coating sensation is evoked by the addition of hydrocolloids such as xanthan gum and locust bean gum, carrageenan [14,15], and fat-containing food materials such as dairy fat emulsion [15]. However, several studies have reported that low-molecular-weight compounds enhanced the intensity of mouth coating. Dawid and Hofmann reported that 1,2-dithiolan-4-carboxylic acid 6-D-glucopyranoside ester exhibited a buttery mouth-coating sensation [16]. Additionally, the same research group demonstrated that polyphenolic compounds such as vanillin, vanillin-related compounds, americanin

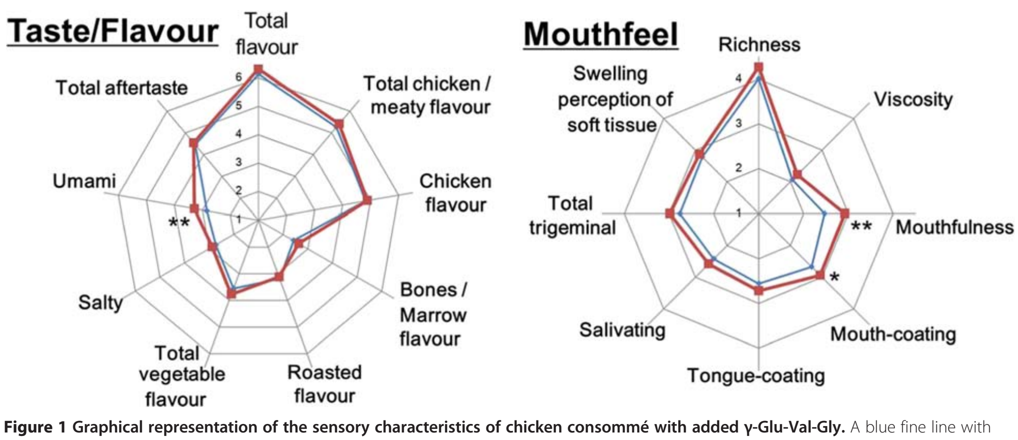

Figure 1 Graphical representation of the sensory characteristics of chicken consommé with added γ-Glu-Val-Gly. A blue fine line with diamond symbols indicates the mean scores of the control consommé. A red bold line with square symbols indicates the mean scores of the consommé with added 5 ppm of γ-Glu-Val-Gly. Asterisk denotes significance at a 95% confidence level; double asterisks denote significance at a 99% confidence level.

A, and 4′,6′-dihydroxy-3′,5′-dimethoxy-[1,1′-biphenyl]-3-carboxaldehyde from cured vanilla beans exhibited a velvety mouth-coating sensation [17]. Furthermore, it has been reported that the flavon-3-ol glycosides such as kaempferol glycosides, quercetin glycosides, myricetin glycosides, and apigenin glycoside from black tea induced a mouth-coating sensation [18]. Despite these observations, there have been no reports of a peptide which exhibited the mouth-coating sensation. Therefore, this is the first report which has demonstrated the mouth-coating effect of peptides. Although the viscosity of consommé did not change significantly by adding 5 ppm of γ-Glu-Val-Gly (data not shown), an enhancement of the mouth-coating sensation was observed. The mechanism of this enhancement is interesting and should be clarified by further investigations.

In the present study, the addition of γ-glutamyl-valyl-glycine enhanced the intensity of umami, mouthfulness, and mouth coating. On the other hands, it has been reported that MSG, representative umami compound, also enhances the intensity of mouthfulness and the sensation related to mouth coating [13]. Previously, it has been demonstrated that γ-glutamyl-valyl-glycine enhanced the umami intensity when it was added to 0.3% MSG solution [3]. In addition, as shown in Table 3, the analysis of the chemical components revealed that chicken consommé contained glutamic acid (51.1 mg/dl) and IMP (21.3 mg/dl), and these concentrations of umami components were sufficient to evoke the umami sensation [13]. Therefore, it was considered that the enhancement of mouthfulness and mouth coating by γ-glutamyl-valyl-glycine was possibly caused by the enhancement of the function of the umami components. Regarding difference between the function of *kokumi* compounds and umami compounds, it was considered that the unique character of the *kokumi* compounds is that *kokumi* compounds have no taste themselves. Therefore, it can be assumed that *kokumi* compounds can enhance sensations like mouthfulness and continuity in sweet foods. In our recent study, it was observed that γ-glutamyl-valyl-glycine enhanced aftertaste, oiliness, and mouthfulness in reduced-fat peanut butter [19]. This result suggest that *kokumi* compounds can be used both in savory foods and sweet foods, while umami compounds can be used mainly in savory foods because of the characteristic umami taste. Further detailed studies are necessary to clarify the mechanism of the enhancement of the mouthfulness and mouth-coating sensation by γ-glutamyl-valyl-glycine.

The addition of γ-Glu-Val-Gly significantly enhanced the intensity of umami, mouthfulness, and mouth coating in chicken consommé. The results suggest that adding γ-Glu-Val-Gly can improve the flavor and mouthfeel of chicken consommé. To confirm this possibility, consumer preferences for chicken consommé with added γ-Glu-Val-Gly are now being investigated in our laboratory.

Table 3 Contents of free amino acids and 5′-nucleotide in chicken consomme

Component	Content (mg/dl)
Amino acids	
Taurine	74.9
Aspartic acid	17.5
Threonine	27.5
Serine	20.3
Glutamic acid	51.1
Glycine	15.8
Alanine	23.6
Valine	10.2
Methionine	4.7
Isoleucine	7.0
Leucine	12.4
Tyrosine	9.9
Phenylalanine	8.0
Lysine	17.0
Histidine	6.6
Arginine	23.7
Hydroxyproline	2.5
Proline	10.0
5′-Nucleotide	
5′-IMP	21.3
5′-GMP	N.D.

N.D. not detected.

Conclusions

In the present study, the sensory characteristics of chicken consommé with 5.0 ppm added γ-Glu-Val-Gly were investigated using descriptive analysis. Chicken consommé containing γ-Glu-Val-Gly had significantly stronger "umami" and "mouthfulness" (mouth-filling sensation) characteristics than the control sample at a 99% confidence level and significantly stronger "mouth-coating" characteristic than the control at a 95% confidence level. These data indicated that a *kokumi* peptide, γ-Glu-Val-Gly, can enhance umami, mouthfulness, and mouth coating in chicken consommé. From these results, it was suggested that the addition of γ-Glu-Val-Gly can improve the flavor and mouthfeel of chicken consommé.

Methods

Preparation of γ-Glu-Val-Gly

The γ-Glu-Val-Gly used in the present study was of food additive grade (FEMA-GRAS No. 4709; JECFA food flavoring No. 2123) obtained from Ajinomoto Co., Inc. (Tokyo, Japan) and was prepared by a chemical synthetic method reported previously [3].

Preparation of chicken consommé

The raw materials for chicken consommé are shown in Table 4. Minced chicken breast meat, minced chicken leg meat, and egg white were mixed. Then, minced chicken wing meat was added and mixed. The raw materials (except bouillon and water) were mixed in a 60-l aluminum pot. Bouillon (Kisco Co. Ltd., Tokyo, Japan) diluted with the same volume of water was added and boiled at between 90°C and 95°C for 30 min. After removing the meat, precipitate, and fat, the resulting chicken consommé was freeze-dried (freezing temperature, −24°C; vacuum <13 Pa; sample temperature, <20°C) using a Freeze Drier (RL-50 MB, Kyowa Vacuum Engineering Co. Ltd., Tokyo, Japan). For sensory evaluation, 5.6 g of the freeze-dried chicken consommé powder and 0.2 g of sodium chloride were dissolved in 100 ml of distilled water and heated to 60°C and presented to the panelists. Approximately 90 ml of consommé was served in foam cups coded with three-digit random numbers.

Selection of the panel

Eighteen female panelists participated in the sensory evaluation. The age of the panelists was 54.0 ± 8.8 (mean ± standard deviation) years old. They all live in the San Francisco Bay Area, CA, USA. The screening of the panelists was conducted in three phases: phone screening of applicants, on-site acuity testing, and face-to-face interviews with advanced acuity testing.

Table 4 Raw materials for the chicken consommé

Materials	Weight (g)
Chicken breast meat (minced)	6,818.2
Chicken leg meat (minced)	6,818.2
Chicken wing meat (minced)	6,818.2
Egg white	1,500.0
Fried onion	1,687.5
Carrot	562.5
Celery	375.0
Tomato	1,406.3
Tomato paste	150.0
Parsley	18.8
Black pepper	5.6
Bouillon (Kisco Co., Inc.)	15,000.0
Water	15,000.0

Training of the panel

General panel training

All of the panelists were broadly trained in sensory descriptive analysis to evaluate aromas, flavors, textures, and appearance across a wide range of consumer products. This training was conducted for approximately 3 days per week for 3 months, during which the panelists expanded their food sensory vocabularies, learned to use a 15-point scale to rate attribute intensities, and evaluated a wide variety of foods. For example, the sweetness intensity scale was anchored with several concentrations of sucrose in water and the intensity of “sweet aromatic” was anchored with several concentrations of vanilla in milk. The panelists-in-training refined their skills by participating in practice tests using many different types of products. After each test, they were given detailed feedback while retesting the products to help them improve their performance. After this training was complete, the panelists were registered as members of the Descriptive Panel of The National Food Laboratory and began to participate in the descriptive analysis of various kinds of foods.

Ongoing panelist feedback

Feedback was routinely provided during panel sessions to maintain and refine the evaluating ability of the panelists. Several times a month, the panelists were given face-to-face performance feedback to help them maintain their calibration. A panel leader tasted the products with the panelists as they reviewed their scores to highlight potential areas for improvement. Feedback was given both on discrimination among products and consistency between replications.

Project-specific orientation sessions

The objectives of the orientation training sessions were to understand the effect of γ-Glu-Val-Gly on chicken consommé to generate the list of sensory attributes for the evaluation sessions. This 2-h training session was conducted on the day before the sensory evaluation for the present study. During the session, panelists evaluated samples of chicken consommé with and without γ-Glu-Val-Gly to understand the effect of γ-Glu-Val-Gly. A panel leader led the group in discussion on the differences and similarities between the samples. They developed a list of sensory attributes that described the products’ sensory characteristics, focusing on attributes believed to be influenced by γ-Glu-Val-Gly. Each sample was tested at least twice during this orientation session. During this training session, the panelists also developed new attributes such as “total chicken/meaty flavour”, “bones/marrow flavour”, “roasted flavour”, “richness”, “tongue-coating”, and “salivating”. Overall, the panelists defined the 17 sensory attributes listed in Table 2. The panelists practiced rating the samples on the list so that they were prepared to begin data collection.

Project-specific panelist feedback

Between each of the six data collection replications, panelists were given feedback about the samples they had evaluated. A panel leader led the group in brief discussions on the differences and similarities between the samples. Panelists were instructed to taste samples (with and without 5 ppm γ-Glu-Val-Gly) for training purposes during the discussions. After each feedback discussion, the panelists took a 10-min break before data collection for the next replication.

Procedure for sensory evaluation

For the evaluation of chicken consommé, panelists held the product in the mouth for 10 s, expectorated, and then rated flavor, texture/mouthfeel, and aftertaste attributes. They then completed the rating for each attribute (samples with and without 5 ppm γ-Glu-Val-Gly) on a 15-point line scale. The sample serving order was balanced, with each sample being presented approximately an equal number of times in each position for each test. Two days of data collection were completed, each consisted of three replications. Feedback to the panelists was provided after each replication except the final replication. In total, six evaluations were conducted. In the present report, to investigate the effect of γ-Glu-Val-Gly on chicken consommé by an experimental protocol after a single feedback session, we report the result of the second replication of sensory evaluation data, which followed the first panelist feedback session on the first day of data collection. Human sensory analyses were conducted following the spirit of the Helsinki Declaration, and informed consent was obtained from all panelists. The experimental protocol was approved by the ethics board of the Institute of Food Sciences and Technologies, Ajinomoto.

Analyses of free amino acids and 5′-nucleotides in chicken consommé

Free amino acids were determined using a Model L-8800 amino acid analyzer (Hitachi Corp., Tokyo, Japan) with a lithium citrate buffer (PF-series for nonhydrolyzed amino acid analysis; Mitsubishi Chemical, Tokyo, Japan). The contents of 5′-nucleotides were determined by HPLC equipped with a Hitachi #3013 column with detection at 254 nm.

Statistical analyses

Statistical analyses were conducted using JMP version 9.0 (SAS Institute Inc., Cary, NC, USA). The data were collected as the means ± standard deviation. Data were assessed by the paired *t* test. The data was considered to be significant when the confidence level was more than 95%.

Abbreviations

γ-Glu-Val-Gly: γ-glutamyl-valyl-glycine; GSH: glutathione; CaSR: calcium-sensing receptor; FEMA: Flavour and Extract Manufacturers Association; JECFA: The Joint FAO/WHO Expert Committee; MSG: monosodium glutamate; IMP: inosine monophosphate.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MK, NM, and TK conceived the idea of this study. TM, MK, and NM designed the detail of experiments. TM and HK conducted the sample preparation and sensory evaluation. TM and MK conducted the analysis of sensory data and wrote the manuscript. All authors read and approved the final manuscript.

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