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Flavour Perception and Satiation

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Abstract:

Taste, smell and texture influence food palatability and intake as we tend to consume the foods we like, and avoid the foods they dislike. Beyond palatability, sensory signals like taste, smell and texture inform learning and acquire their meaning through the physiological and psychological consequences of eating and can have a dramatic impact on satiation, satiety and the regulation of energy intake. Smell stimulates appetite and identifies food sources, taste signals the arrival of nutrients and the onset of satiation and food texture moderates the rate of eating and oral-metering of calories by the senses. In our highly palatable food environment, subtle differences in sensory quality, intensity and texture can influence everyday eating behavior and energy intake independently of liking. The chapter provides a summary of recent developments in our understanding of how sensory properties influence the onset of satiation and implications of these findings for energy intake and food development.

1.0 Introduction:

Foods and beverages comprise complex mixtures of volatile, non-volatile, visual, structural and irritant information that is detected independently by each of the different senses, and integrated into a single perceptual impression that informs food palatability and intake behaviour. Sensory properties are likely to be operational before and during food intake and have an early impact on acute energy intake within a meal, often occurring in advance of the endocrine or visceral signals that prompt the end of a meal. Satiation describes the processes associated with meal termination, and factors affecting satiation are likely to determine how much a person consumes within a given eating occasion. Much of the previous research on sensory influence on satiation has described the role of pleasantness, palatability, sensory specific satiety and alliesthesia in guiding energy intake within a meal (Cabanac, 1971, De Graaf, 2005, Mela, 1999, Rolls et al., 1984, Yeomans, 1998). However, eating behaviour and acute energy intake are driven by factors beyond simply eating more of the foods we like and less of the foods we dislike. Visual, textural and flavour cues can be used to signal the potential post-ingestive consequences of food consumption, guiding our daily food choices, appropriate portion selection and the habitual meal and dietary patterns that result in healthy or unhealthy diets. When considered in this way, a deeper knowledge of the sensory influences on food choice, acceptance and intake are central to our understanding of energy intake regulation. This chapter aims to present new perspectives on functional aspects of sensory perception that can be applied to improve satiation, enhance satisfaction and reduce overall energy intake overtime.

Food palatability is shaped in response to the frequency of consumption and the prevalence of sensory experiences in the food environment, and there is circularity between food preferences and habitual dietary behaviours. A good example of this is the development of a lower preferred level of salty taste in foods following a sustained period on a low salt diet (Bertino et al., 1982). This means that the pleasantness associated with eating a food can be acquired and re-acquired throughout the lifespan in response to changes in our food environment and dietary experiences. Evidence that food palatability promotes energy intake is clear and has been summarized elsewhere (Yeomans, 1998, Sorensen et al., 2003), but this is not the whole story. Above a certain level of acceptance, the rated liking for a food is no longer predictive of the amount of food consumed, indicating that liking may be predictive of initial motivation to eat, but not of the total amount of energy consumed (De Graaf et al., 2005). Palatability is sometimes used as a catchall term that integrates the various sensory properties of a food, summating them to a single judgment of liking. Changes in the overall sensory intensity also contribute to reported changes in intake behaviour beyond their influence on food palatability. The real-world relevance and application of the relationship between palatability and food intake is questionable in the modern food environment where we are surrounded by an ever increasing variety of highly palatable foods. In a world of palatable food everything becomes acceptable and the usefulness of palatability in explaining differences in energy intake becomes somewhat diminished. In terms of the role of flavour in promoting satiation, most effort has been placed on understanding how sensory properties can be optimized to increase food enjoyment, while much less attention has been given to optimizing sensory cues to promote fullness and curtail energy intake. A foods sensory properties contribute to much more than acceptance, informing choice by signaling nutrient content while also moderating the way a food is eaten and preparing the body for the arrival of energy and nutrients. In recent years researchers have moved beyond hedonic dimensions of food intake to explore energy intake when sensory qualities and intensities are manipulated in equi-palatable foods. The following sections explore the recent developments to understand how odour, taste and texture can be used to influence energy intake.

2.0 Impact of Food Odour on Food Intake and Satiation:

Food odours help to identify suitable food sources for consumption and stimulate our desire to eat. Odours are key in shaping our memories of consumed foods and beverages and recalling their satiating effects (Herz and Engen, 1996) and through stimulating appetite and informing portion selection.

2.1: Impact of Food Odour on General Appetite

Food odours have been shown to influence food choices, portion selection and can promote a specific desire to consume certain foods (Ferriday and Brunstrom, 2008). Even when satiated, the sight or smell of a desirable food can stimulate appetite (Cornell et al., 1989). People that exhibit a higher level of dietary restraint have been shown to be more responsive to food odour cues, resulting in a higher appetite and desire to consume the cued food item (Fedoroff et al., 2003, Fedoroff et al., 1997). Others have suggested exposure to a desirable savoury odour increases reactivity and attention to all food, leading to a general desire to eat (Ferriday and Brunstrom, 2008). Frequently, these studies focus on responsiveness to energy dense, highly palatable foods such as pizza or ice-cream. In this sense, responsiveness to energy dense foods may be one important mechanism that promotes energy intake by stimulating appetite by increasing the number of eating events, and types of foods selected. A similar phenomenon has been described as non-homeostatic hunger or ‘hedonic hunger’, where susceptible individuals are more sensitive to food cues and seek food spontaneously, eating for pleasure irrespective of any underlying need (Lowe and Butryn, 2007). Individual differences in appetitive responsiveness to rewarding properties of the food environment can be measured using the ‘power of food scale’, which also suggests that for some people, food odour is a very powerful stimulus that can motivate eating in the absence of hunger, snacking and promote positive energy balance (Lowe et al., 2009).

2.2: Impact of Odour on Food Choice and Sensory Specific Appetites

In recent years several authors have re-evaluated the impact of odour cues on choice and intake to clarify how odours promote appetite for the cued food and whether this results in greater food intake (Gaillet-Torrent et al., 2013, Gaillet-Torrent et al., 2014, Ramaekers et al., 2014b, Ramaekers et al., 2014a, Zoon et al., 2014). These studies have demonstrated an insignificant change in overall intake, but significant changes in appetites for specific sensory attributes and subjective feelings of hunger and fullness. In one such study, food odours had a small impact on general appetite, but promoted desires for the specific foods that were cued, such as tomato soup from tomato odour and banana dessert from iso-amyl acetate (Ramaekers et al., 2014a). Interestingly, in their study non-food odours decreased general appetite, savoury odours increased the desire to consume savoury foods, but also decreased the appetite to consume sweet foods (Ramaekers et al., 2014a). The reverse relationship also held, where sweet odours stimulated a desire to consume sweet foods and showed a decreased appetite for savoury foods. The effect of odor exposure was examined for its impact on general appetite and for ‘sensory-specific appetite’ using a series of food and non-food odours (Ramaekers et al., 2014a). Contrary to previously reported findings, the authors failed to demonstrate the development of odour-sensory specific satiety (Rolls and Rolls, 1997), despite extended stimulation with the same odours (>12mins). In a follow up study, the odour stimulus was changed spontaneously and changes in sensory specific appetites were also recorded. Sensory specific appetites for sweet and savoury foods changed when the odour shifted from sweet to savoury, but what was striking was the speed with which specific appetites for sweet or savoury food items switched as this occured with in milli-seconds (Ramaekers et al., 2014a). When combined with the fact that odours strongly stimulate the cephalic phase response to food (Teff and Engelman, 1996), this suggests that the nexus between the olfactory and appetitive systems is highly sensitive to environmental changes with a strong inter-connection uniting the system that identifies a food source and the system that prepares the body for its arrival.

Recent findings from a rodent study also highlight that preference for an initially disliked stimlulus (quinine) can be increased following pre-exposure to an odour (lemon) among new born rats, indicating that odour learning can have an immediate and lasting impact on intake behaviour (Kamenetzky et al., 2014). This evidence suggests odour cues can signal the consequences of consuming a food and sensitivity to an odour may be predicated by an individuals physiological need state and the anticipated benefit of (Boesveldt et al., 2014). If this is the case, we would expect that the appetitive response to certain odours signaling the presence of high and low energy food items may be moderated by our homeostatic need for energy. This was tested to explore whether there is an interaction between hunger and liking for ambient food odours that were associated with high and low energy foods (Zoon et al., 2014). Overweight participants tended to be less effected by their hunger than normal weight participants, however for both groups, ambient odour exposure did not influence hunger or food intake. When considered with the findings on food cue exposure and hedonic hunger above, it may be that ambient food related odours primarily influence energy balance by stimulating specific appetites and promoting food intake.

In the studies described odour presentation was usually pronounced and noticeable, but within the natural environment we are surrounded by thousands of volatile chemicals that are unconciously perceived. A series of studies have examined the effect of these ambient 'non-attended' odours and how they influence food choice and intake at a meal. In the first of these, subjects were exposed to either a melon or pear odour in a waiting room before selecting food items from a menu (Gaillet-Torrent et al., 2013). After exposure to the fruit odours participants were more likely to select desserts with fruit, but not starters or main courses. The authors suggest a quality specific priming effect of each odour that influenced food choices. In a later experiment the odour priming was repeated and was shown to influence actual food choices at a buffet meal, where a pear odour promoted selection of a fruit salad over a non-fruit alterenative, though there were no reported differences in food intake in either condition (Gaillet-Torrent et al., 2014). Overall, whether consciously perceived or not, food odours seem to have an important mediating effect in promoting hedonic hunger, influencing food choice and stimulating sensory specific appetites.

To date no studies have successfully demonstrated a reduction in food intake using food odours in this way, though when considered as a cue that motivates spontaneous consumption behaviours, odours can stimulate appetites and intakes for certain foods (Fedoroff et al., 2003, Fedoroff et al., 1997, Ferriday and Brunstrom, 2008). Effects demonstrated to date are heavily influenced by the quality and intensity of the odours presented, the test context and food stimuli. Some studies have also failed to demonstrate the appetitive effects of odours when using different stimuli and contexts (Nowlis et al., 2008). Importantly, there are only five basic tastes, but thousands of food related odours in our environment making it impossible to attend to all in a conscious manner. It is likely that odours primary role is to stimulate food intake and to help discern food sources while navigating a complex food environment. Further research is required to understand how universally the stimulation from odours can impact food intake.

2.3: Odour Perception and Satiation

Changes in the ambient odour of a feeding environment can stimulate appetites, but is it possible to reduce food intake while eating by changing the quality and intensity of aromas that are perceived retro-nasally? This is an attractive proposition for controlling calories, as odour volatiles impart a lot of flavour and increase liking, yet contribute very little energy to a food. Throughout the consumption of a meal, food odours are released as 'aroma' through mastication and volatile release as odour chemicals are perceived retro-nasally by the olfactory epithelium (Delahunty and Saunders, 2003). The food matrix and an individual's chewing efficiency influence the quantity and quality of odours released and influence the duration and intensity of the aromas perceived.

In recent years extensive research has focused on understanding how this release pattern develops, and whether or not retro-nasal sensory stimulation can promote satiation and reduce food intake. In a series of studies, Rianne Ruijschop tested whether higher intensity of aroma and increased aroma stimulation can influence feelings of fullness and food intake within a meal (Ruijschop et al., 2008, Ruijschop et al., 2009a, Ruijschop et al., 2009b, Ruijschop et al., 2010). Most of these studies manipulated the aroma intensity and duration of odour delivered retro-nasally via an olfactometer. Obese individuals are thought to eat faster, and so the question was whether there are aroma release profile differences between lean and obese and if so, could this account for the increased energy intake that leads to weight gain. However, findings showed that the aroma release profile is a physiological feature of an individual, with no distinct release pattern in one BMI group (Zijlstra et al., 2011). Aroma release increases from liquids to semi-solids to solids as each requires further mastication before swallowing (Ruijschop et al., 2008). Subjects report significant increases in the subjective feelings of fullness when delivered an aroma, and their desire to eat a sweet product was decreased following strawberry odour delivery. Further studies showed a negative trend between the extent of retro-nasal aroma released, quantified using APCI-MS, and the amount of ad-libitum food intake (Ruijschop et al., 2009a, Ruijschop et al., 2009b). In addition to intensity and duration, the authors went on to explore the role of odour mixture ‘complexity’, through exposure to multiple aroma components of the same quality, and again reported subtle changes to subjective feelings of satiation (Ruijschop et al., 2010). However, despite promising findings of increased feelings of fullness across the series of studies odour stimulation failed to significantly impact within meal food intake in a consistent manner. A recent paper had subjects consume a tomato soup and used an olfactometer to deliver a tomato odour via retronasal tube with long and short odour duration in high and low intensity (Ramaekers et al., 2014c). Those in the long duration, high intensity condition consumed on average 9% less soup. Although these findings suggest it is possible to enhance the onset of satiation and reduce food intake with odours, they have yet to be replicated under normal eating conditions. This, combined with the inconsistency and small effect sizes reported in the previous work, suggests that retro-nasal odour stimulation may have a limited effect on ad-libitum intake, and there are significant challenges in engineering odour release profiles to prompt these effects in real food systems under natural eating conditions.

Beyond food selection and intake, perceived aroma intensity during consumption has also been shown to influence how a food it is eaten (De Wijk et al., 2012). Higher aroma intensity led to smaller bite sizes and influenced subsequent bites showing a sub-conscious adaptation to the perceptual intensity and quality, based on the sensations experienced ortho- and retro-nasally during eating. Whereas the important role of odours in food choice and intake is acknowledged, the effect sizes are relatively small and the application of these findings to curtailing food intake remains an elusive challenge to implement in real food systems.

3.0 Impact of Taste on Food Intake and Satiation:

The five basic taste properties combine with aroma to form flavour and together inform food choice and intake and although we may respond to individual tastants this is rarely the case as virtually all foods and drinks comprise mixtures of taste stimuli that interact (Keast and Breslin, 2003). Basic tastes are often classified by their aversive or appetitive effect on intake, depending on the anticipated effect they will have upon ingestion. For example, sweetness helps to identify energy-rich foods, while bitterness serves as a warning sign of poisons (Miller, 2011).

When the taste system is by-passed and food enters the stomach without being perceived on the tongue, satiation and reward value of the ingested calories are lower, highlighting the importance of taste in the development of satiation (Cecil et al., 1998, Spetter et al., 2014, Wijlens et al., 2012). Exploring how specific tastes influence food intake can be challenging as it is difficult to independently separate taste quality and intensity from palatability and energy content. In addition, many volatile flavour compounds are referred to as 'tastes' in a process of taste referred olfaction (Murphy et al., 1977). It is also likely that for highly congruent taste-smell combinations, the taste-referred olfaction may be a form of learned 'synesthesia', where qualities from one sensory system evoke qualities in another through their frequent co-occurrence (Prescott, 1999). In this section, we discuss the impact of taste quality and intensity on food intake.

Several attempts have been made to characterise dietary intake behaviours by the predominance of specific taste qualities in habitual food intake patterns. These approaches combine traditional sensory techniques with dietary epidemiology to establish meaningful links between food sources of healthy or unhealthy nutrients as a function of their predominant taste quality (Cicerale et al., 2012, Cox et al., 2015, Mattes, 1985, Mattes and Mela, 1986, Viskaal-van Dongen et al., 2012). In the US it is estimated that nearly half of all energy comes from 'sweet' foods, 40% from salty / umami (savoury) foods with the only 9% from sour and <5% from bitter (Mattes, 1985). Energy is predominantly delivered by sweet foods and beverages and savoury meals, whereas energy poor bitter and sour fruits, vegetables and beverages such as water, tea or coffee, contribute nominally to the overall energy intake, despite their large contribution to the sensory quality of the diet.

3.1 Bitter: The dietary patterns associated with bitterness perception have been extensively studied as researchers try to find a meaningful link between the bi-modal distribution of bitterness sensitivity in the population and subsequent energy or nutrient intake patterns. Proponents of the bitter tasting compound 6-n-propylthiouracil (PROP) theory of dietary behaviour suggest that an increased sensitivity to bitterness, determined by an individual's sensitivity to PROP, results in the rejection of foods high in bitter compounds such as glycosides, alkaloids and phenolic compounds (Drewnowski et al., 2000, Duffy and Bartoshuk, 2000, Bartoshuk, 2000). Findings have associated higher PROP sensitivity to lower body mass index levels, with non-tasters and medium tasters correlated as heavier than supertasters, (Tepper and Nurse, 1998). However, other studies have suggested the opposite (Oftedal and Tepper, 2013), while some authors have suggested that PROP status may contribute to energy reductions in lifestyle interventions, suggesting a wider interaction with energy intake beyond the diet (Coletta et al., 2013). Nevertheless, many strongly bitter products are oftentimes well liked and frequently consumed by those with strong bitter sensitivity (Drewnowski and Rock, 1995, Guinard et al., 1996, Mattes, 1994). Many PROP sensitive individuals still enjoy black coffee or the bitterness of a Gin and tonic, questioning the proposed linearity between taste sensitivity and food and beverage preferences. Food preferences evolve through repeated experience and consumption and it seems unlikely that the complexity of human dietary behaviour can be summarised and explained by the differential sensitivity to a single taste quality in the diet. Given the energy content of bitter foods is typically much lower than that found in savoury or sweet foods; a sensitivity to PROP is unlikely to significantly influence overall daily energy intakes.

3.2 Sour: Research on the influence of sourness on energy intake has been focused mostly on understanding the acceptance and intake of fruits among young children. This research has highlighted the importance of dietary learning and experience on the acceptance and intake of sour fruits (Liem and Mennella, 2002). Children fed on formula containing sour tasting protein hydrolysates tended to have a higher acceptance and intake of sour foods and higher concentrations of citrate in orange juice (Liem and Mennella, 2002). Similarly, children tend to have a higher sour preference during childhood (Liem and Mennella, 2003). To date, the application of sourness intensity has not been studied as stimulus in adults in relation to its impact on food intake or the onset of satiation. Moreover, similar to bitterness; many sour foods tend to have lower energy density and are unlikely to contribute significantly to overall energy intake.

3.3 Salt: Salt enhances palatability and can motivate intake but may also play an important role in terminating food intake. The impact of salt intensity on satiation and energy intake within a meal has been explored in a series of studies using tomato soup. Equally palatable tomato soups were produced that had perceptibly different levels of salt intensity (Bolhuis et al., 2012). Each subjects preferred salt concentration was painstakingly measured by plotting a dose response psycho-hedonic function, and then the salt intensity was raised and lowered per participant to ensure perceptible intensity changes in equally palatable versions of the tomato soup. In the first of these studies, salt intensity had no impact on ad-libitum intake when soup was the only food served to a group of hungry participants (Bolhuis et al., 2010). In a follow up study, soup was served with an ad-libitum sandwich lunch and energy intake was 8% lower in the high salt condition compared to the low salt condition. The authors concluded that increasing the salt intensity resulted in an increase in the sensory exposure, producing a faster satiation during consumption, per kcal consumed (Bolhuis et al., 2011). When equi-palatable soups with low or high salt intensity were again served and combined with long or short oral duration times (eating rates) controlled using a peristaltic pump, a decrease of 9% in energy intake was observed for the higher salt intensity compared to the lower salt intensity (Bolhuis et al., 2012). The most significant effect however was a 34% decrease in intake when high salt intensity was combined with longer oral duration time, showing for the first time that an increase in intensity and a longer exposure to the taste qualities in mouth produced the strongest satiating effect. In all conditions, there were no differences in participant's ratings for hunger or fullness, indicating the energy reduction was achieved without a loss in satisfaction for the meal. Together, these studies represent the first attempt to use taste intensity to reduce energy intake within equally palatable versions of the same meal.

In an older study that sought to explore the onset of sensory specific satiety for weak and strong tasting for iced teas, Vickers and Holton noted that the stronger tea was consumed less, although the decrease in liking (SSS) for both teas was equivalent (Vickers et al., 1998). The results were attributed to the initial liking of the teas, but perhaps with the new insights from the Bolhuis findings the reason for decreased intake may have been due to the higher intensity of the taste solutions, independent of their impact on SSS. Taste intensity seems to have an impact on the rate of satiation and may influence overall energy intake, when palatability has been controlled. In another study there were no differences in the rate of decline of desire to consume or overall intake of calories for sweet and savoury rice meals with equivalent palatability, texture, energy density, and macronutrient composition (Griffioen-Roose et al., 2009). In this regard, taste intensity and oral duration seemed to have a much stronger effect than differences in taste quality alone.

3.4 Umami: Umami has been recognized as a distinct taste for over 25 years and is associated with the potent taste enhancing peptide salts that occur naturally throughout the food supply. Umami imparts ‘deliciousness’ and is a central flavour component of many cuisines all over the world, from the dashi broths of Japan to the sun dried tomatoes and parmesan cheeses of Italy. The importance of umami in stimulating palatability, appetite and nutrient signaling has been associated with individual sensitivities to this taste in foods (Hermanussen et al., 2006, Murphy, 1987), where sensitivity may be acting to reflect underlying changes in protein status (Luscombe-Marsh et al., 2008). There have been suggestions that umami sensitivity may be linked to differences in BMI (He et al., 2008, Kondoh and Torii, 2008) and recent findings from Pepino and colleagues highlight that obese women have been shown to be less sensitive to MSG (Pepino et al., 2010). Epidemiologically it seems unlikely that obesity rates can be explained by MSG sensitivity, given the prevalence of this taste quality throughout Asia and the low rates of obesity in this region (Shi et al., 2010).

Others have suggested umami signals the presence of protein in foods and link higher food intake and positive energy balance to the need to consume more food to compensate for the poor quality of protein in the modern food supply (Simpson and Raubenheimer, 2005). This suggests that individuals who are deprived of protein should increase in their preference for and sensitivity to umami and related compounds in foods that signal the presence of protein. After a severe protein deficit, food intake and food and odour preferences were directed more towards protein rich foods, suggesting a possible adaptive compensatory mechanism to restore protein status (Griffioen-Roose et al., 2012). It is unlikely that such extreme protein deficit would be commonly encountered in an abundant modern food environment but this study highlights a functional role of the chemical senses in guiding food intake behaviours to maintain protein balance and overall homeostasis.

Umami has been reported to both stimulate and curtail the desire to eat (Masic and Yeomans, 2014a). Studies have explored the impact of umami on short term appetite and found weak effects of MSG-supplemented soups on intake within a meal (Rogers and Blundell, 1990), although subjective appetite ratings indicated that hunger returns faster in the MSG condition. Others have suggested a ‘second meal effect’, where there was no impact of MSG on intake within the test meal, but intake was higher at a second meal (Luscombe-Marsh et al., 2009). In a double blind, double pre-load paradigm, Carter and colleagues showed no differences on energy intake within a meal for an MSG-IMP soup although consistently there are differences in subjective appetite and motivational ratings post meal (Carter et al., 2011). The implication is that umami increases palatability and desire to eat, but does not change overall energy intake within meal. But does an umami meal with protein leave you feeling fuller between meals? In a series of studies, Masic and Yeomans have explored the link between umami taste and the macronutrients delivered (Masic and Yeomans, 2013, Masic and Yeomans, 2014a, Masic and Yeomans, 2014b). Using a pre-load paradigm participants were served carbohydrate or protein rich soups with and without MSG. Energy compensation is greatly improved when MSG is paired with a protein based soup, indicating that when the sensory properties align with the nutrient content of the food ingested it is easier to detect calories. MSG has also been suggested to influence gastric emptying rates from foods of equivalent protein contents (Zai et al., 2009). The suggestion that MSG may have a 'biphasic' effect on motivations to eat seems plausible given its contribution to palatability and motivation to consume within a meal and the recent findings suggesting an important effect in promoting satiety during the inter-meal period (Blundell and Rogers, 1991, Masic and Yeomans, 2014b, Rogers and Blundell, 1990). Importantly, these studies are central to our understanding of flavours role in satiation and satiety as tastes that influence palatability can also interact with nutrients in the food to stimulate a stronger or weaker physiological response. To date, no study has explored the impact of increased taste intensity of umami in promoting satiation, using the same approach as Bolhuis work on salt (Bolhuis et al., 2011). Given its intense flavour and relationship with nutrient signaling it would be worthwhile exploring the relationship between umami intensity and satiation in the future. The concept that a taste signal on the tongue can enhance the satiating properties of a food is highly appealing, as umami contributes small amounts of energy but may significantly enhance the consumer experience by sustaining fullness for lower energy.

The palatability enhancing effect of umami compounds has also been suggested as a possible approach to compensating for chemosensory loss among the elderly. Early research provided support for flavour enhancement of foods for the elderly with MSG shown to enhance enjoyment, increase food intake and reverse anorexia of aging among elderly (Mathey et al., 2001, Schiffman, 2000, Schiffman and Warwick, 1988, Schiffman and Warwick, 1989, Schiffman and Warwick, 1993, Essed et al., 2007). However, subsequent longer-term interventions have shown little or no impact of MSG flavour enhancement on food intake or nutritional status, with the authors concluding that the chemosensory heterogeneity of the elderly population requires a more individualized approach to flavour enhancement to motivate intake (Essed et al., 2009).

It is difficult to reconcile the proposed dual function of MSG as both appetite stimulant and suppressor, when on the one hand umami can sharpen the regulation of food intake and digestion, while on the other it can stimulate appetites and food intake among vulnerable populations (Mouritsen, 2012). These questions remain today, yet clearly there is a need for further studies that demonstrate a lasting impact on energy intake and a proposed mechanism beyond the palatability dimension of better-tasting and more flavoursome meals. To date, no study has successfully demonstrated a meaningful or consistent increase or decrease in energy intake within or across meals that can be attributed to umami intensity. Unlike olfaction, there are clear links between taste perception on the tongue and the nutrient quality of foods being consumed, highlighting the important interaction between pre- and post-ingestive events that inform preference learning and the formation of fullness expectations.

3.5 Sweet: Sweetness contributes to the palatability and intake of many foods and adding sweet tastants to a food often increases its acceptance (De Graaf et al., 1993). Sweet tasting carbohydrates are also important in moderating glucose flux in the blood and there are clear relationships between sweet perception and insulin secretion (Anton et al., 2010). Excessive calorie intake from sugars has led to the search for alternative sources of sweetness in the diet in the form of non-caloric sweeteners (NCS) such as aspartame, acesulfame-k, and sucralose and in recent years, stevia. Regular consumption of sugar (sucrose) sweetened beverages is strongly associated with weight gain and higher BMIs (Malik et al., 2006). NCS produce very high intensity sweetness and have found extensive application in the soft-drinks industry. This creates an interesting scenario where calorie arrival is signaled on the tongue, but not delivered post-ingestively. The impact of these NCS on energy intake and appetite has been widely researched, to evaluate whether they could be used to reduce energy intake. Early research utilized pre-load paradigms or supplemented the diet with sugar or NCS sweetened beverages to explore how NCS like saccharin and aspartame influenced food intake, finding that sweeteners stimulate appetite but overall led to a reduction in energy intake compared to glucose or sucrose (Mattes, 1990, Rogers and Blundell, 1989, Rogers et al., 1988, Rolls et al., 1988, Tordoff and Alleva, 1990). The consensus is that although NCS do not have the same satiating capacity as glucose or sucrose, they can be used to replace existing sweetness from sugars and effectively reduce overall energy intake to support weight loss (Rolls, 1991). This is supported by longitudinal epidemiological analyses from the Nurses' health study (N= >50,000), which profiled dietary behaviour of adult nurses over 8 years and showed weight increases associated with the consumption of sugar sweetened beverages (Chen et al., 2009). These findings have also been confirmed by extensive systematic reviews (Malik et al., 2006) and meta-analyses (Mattes and Popkin, 2009).

Concerns have been raised that uncoupling of sweet tastes from energy delivery could produce strong rebound hunger and stimulate excess energy intake in response to 'misleading' sensory signals (Swithers et al., 2010). This relationship becomes more complex in the human diet where non-nutritive sweeteners are consumed in the presence of energy from other sources. Much of the research to support an 'uncoupling' argument has been based on rodent models of feeding, which control and simplify the diet to focus solely on sweeteners at the exclusion all other taste qualities. Several longer term NCS trials have now been completed that clearly demonstrate that energy reductions gained by replacing sucrose with sweeteners for periods of up to 18 weeks at a time do not result in later compensation and overall reduce energy intake (De Ruyter et al., 2012, Raben et al., 2002). Only one trial has explored the impact of stevia, aspartame and sucrose on food intake and showed that both stevia and aspartame resulted in reduced energy intake compared to sucrose with equivalent appetite ratings across all conditions. Interestingly, compared to sucrose, glucose levels were lower for stevia and aspartame, and the stevia condition had lower insulin levels than both sucrose and aspartame (Anton et al., 2010). In the context of rising rates of Type 2 diabetes worldwide, it is noteworthy that a NCS not only mimic the perceived sweetness of caloric sugars, but also influence glucose homeostasis post-ingestion. It will be important to explore whether these effects are sustained overtime when such compounds become more widespread and whether the sensory cues and non-nutritive effects interact to inform learning overtime.

Overall, acute feeding and compensation trials, longer-term trials and numerous meta-analyses consistently indicate that the use of low calorie sweeteners do not stimulate hunger but rather result in slightly lower energy intakes when used as substitutes for higher energy-yielding sweeteners (Mattes and Popkin, 2009).

3.6: Potential influence of other taste properties on satiation:

Recent evidence has emerged to suggest that fatty acid tastes are distinct and may constitute a 6th taste. Psychophysical studies have demonstrated that fatty acids of different chain length and saturation can be detected as distinct qualities on their own and have a perceptual character that is independent of other taste qualities (Keast and Costanzo, 2015). Fatty acids are believed to have a distinct transduction mechanism with perception linked to the CD36 taste cells moderated by a G-coupled protein receptor 120 (Running et al., 2015). Ability to detect and rank fatty acids like oleic acid has been linked to fat intake and BMI and suggests a causal link between sensitivity to fatty acid perception, intake and energy balance (Stewart et al., 2010, Stewart et al., 2011). However the perceptual properties of fatty acids remain somewhat poorly defined and debate continues as to whether these subtle differences are truly implicated in energy intake regulation.

Another oro-sensory quality that has been described as a new taste the is the savoury sensation ‘kokumi’ which is associated with the peptide molecules composed of the three amino acids glutamine, valine, and glycine (Toelstede et al., 2009). Kokumi is believed to be a distinct taste quality from the savoury taste umami, though it is also contributes mouthfeel perceptions such ‘continuity / mouthfulness, and thickness’ as well as a general flavor-enhancing effect in savoury foods. This relatively new taste / mouthfeel quality has yet to be studied for its impact on satiation and energy intake but merits further exploration given its links to ‘savouriness’ and potential ability to increase mouthfulness and overall flavour intensity.

The evidence is mounting that taste quality, intensity and the salience of the nutrients and energy they are associated with, play an important role in food intake regulation far beyond tastes impact on food acceptance or palatability. Taste offers the consumer an opportunity to orally meter their energy intake and acts as the bridge between the desire to maintain physiological homeostasis and the desire to eat for pleasure and reward. The finding that taste intensity may stimulate satiation (Bolhuis et al., 2012) offers an opportunity to increase satisfaction by signaling the arrival of macronutrients and calories ingested, while also reducing energy intake without restriction. Central to this is an understanding of how eating behaviours and the rate of transition of tastes through the oral cavity are influenced by the foods and textures consumed.

4.0 Impact of Food Texture on Food Intake:

Food and beverage texture is often overlooked but this important sensory property is central to our appraisal of food quality, freshness and acceptance (Szczesniak, 2002). Texture can influence perception in other modalities by physically impeding the transfer of non-volatile tastants and volatile aroma compounds from the food matrix to the receptors. The physical interaction between food and beverage textures and the release and perception of foods chemosensory properties has been widely researched. These ‘matrix effects’ play an important role in moderating the intensity and duration of sensory properties in mouth (Baines and Morris, 1987, Calviño et al., 1993, Delahunty et al., 2004, Marshall and Vaisey, 1972, Moskowitz and Arabie, 1970, Pangborn et al., 1973).

4.1: Eating Rate, Body Weight and Chronic Disease

Food texture provides a physical barrier to ingestion as foods must be masticated to a degree of size, structure and lubrication that prepares them for safe swallowing (Hutchings and Lillford, 1988). Through this, food texture influences eating rate and in recent years attention has turned to the importance of fast and slow eating rates in moderating energy intake. A meta-analysis of eating rate studies has confirmed that eating rate is associated with higher energy intakes and may be an important contributor to positive energy balance and weight gain (Robinson et al., 2014). Eating rate is believed to be a heritable phenotype (Llewellyn et al., 2008), and it is well established that overweight and obese children tend to have a higher bite rate, fewer chews per bite, and eat faster than non-obese children (0.1-12 years) (Barkeling et al., 1992, Drabman et al., 1979, Chei et al., 2005, He et al., 2000, Laessle et al., 2001, Llewellyn et al., 2008, Fisher et al., 2003). By contrast, chewing thoroughly is associated with a decreased risk of being overweight among children (Ochiai et al., 2012).

Similar findings are seen in larger scale epidemiological studies where higher self-reported eating rates have been associated with an increased risk of obesity (Otsuka et al., 2006), increased BMI (Leong et al., 2011, Maruyama et al., 2008, Sasaki et al., 2003) and an increased likelihood of being pre-diabetic (Mochizuki et al., 2012). Given the established impact on public health, eating rate has been the target for clinical interventions to reduce eating rate and food intake in the treatment of childhood obesity (Ford et al., 2010).

4.2: Food Texture, Eating Rate and Energy Intake

Manipulating the eating rate during a meal has been shown to reduce energy intake. Eating rate studies have tended to use verbal instructions to participants such as chew for longer (Andrade et al., 2008, Li et al., 2011, Martin et al., 2007, Scisco et al., 2011, Shah et al., 2014, Smit et al., 2011, Zhu et al., 2013), or eat as fast as possible for 5 minutes (Kokkinos et al., 2010). In all cases, intake was increased when food was consumed in larger bites, with fewer chews per bite and a shorter oro-sensory exposure time. However to change eating behaviours in a meaningful and sustainable manner, it is first necessary to understand whether food textures can be used to speed up or slow down consumption. In recent years researchers have begun to ask whether food textures such as thickness, hardness or firmness can be used to alter the microstructure of eating and through this influence eating rate and reduce acute energy intake in equally liked food and beverage products (De Graaf, 2012, De Graaf and Kok, 2010). In the first of these studies, Zijlstra and colleagues served participants a chocolate milk (liquid) or custard (semi-solid) and reported a 30% decrease in intake in the semisolid condition (Zijlstra et al., 2008). A follow up study controlled for eating rate and eating effort required to suck the thicker custard through the straw by having samples delivered through a peristaltic pump, and the effect persisted indicating that differences in effort alone did not account for the differences between participants. In a separate study both bite size and the duration of oral exposure were manipulated and participants who ate with larger bites and shorter oral residence times consumed larger amounts of the chocolate drink (De Wijk et al., 2008, Zijlstra et al., 2009a). Similar micro-structural eating patterns have been observed when compared across a wide range of savoury meal components, where those eaten quickly were consumed with large bites, with a short oral duration (Forde et al., 2013a). Texture differences between liquids and semi-solids seemed to have most impact on satiation and the amount consumed within a meal, and less impact post-ingestively on satiety (Zijlstra et al., 2009b).

Eating rate and oral duration time are highly correlated as the longer a food is being chewed in mouth, the longer the oral duration and vice versa. In a clever paradigm, Bolhuis was able to separate out the relative impact of these two variables by setting a fixed eating rate but changing the volume in mouth to change oro-sensory exposure (Bolhuis et al., 2011). When the oro-sensory exposure time was doubled, participants consumed an average of 35 % less, compared to the short oral exposure condition. These effects are surprisingly large, yet the manipulation is simple and straightforward, without the need for the addition of complex ingredients of formulations. Importantly, across all of these studies the focus has shifted away from considering eating rate solely as a property of the consumer, but also as a property of the food being consumed.

Two recent studies have objectively profiled the eating rates of commonly consumed liquids, semi-solids and solid foods (Forde et al., 2013a, Viskaal-van Dongen et al., 2011) and highlight the broad range in eating rates available in the food environment, with liquids consumed up to 600g/min whereas solids were within a range of 10-120g/min. Foods consumed at a higher eating rate were eaten in larger bites, with fewer chews per bite and a lower overall oral exposure (Forde et al., 2013a). This is in line with the proposed mechanism for the effect of eating rate on energy consumption where foods that are consumed in large bites and more quickly, transit the oral cavity and the sensing systems of gustation and olfaction without fully registering their nutrient content (De Graaf, 2012).

The premise is that texture promotes satiation by increasing the time a foods taste and smell properties can signal the arrival of nutrients, though it may also be that the act of chewing promotes fullness and encourages a stronger cephalic phase response. Indeed, several studies have shown that slowing the eating rate during consumption also results in significant changes in the circulating levels of the appetite hormones GLP-1, Ghrelin and PYY (Kokkinos et al., 2010, Li et al., 2011, Zhu et al., 2013). Differences in food texture may also significantly impact metabolic events post-consumption. Rodents fed hard and soft chow diets consumed the same amount of energy over a 6-month period, but soft-fed rodents had greater weight and central-adiposity than controls (Oka et al., 2003). This has been attributed to higher body temperature in hard-fed rats, possibly indicating an increase in dietary induced thermogenesis. Recent findings with humans appear to support the increase in the thermic effect of food when eating slower rather than quickly (Hamada et al., 2014).

Research on eating rate and intake on liquids and semi-solids show large and consistent effects, but most of daily energy is consumed as solid foods within meals. An earlier study on solid foods failed to demonstrate a difference in intake for three solid foods (Zijlstra et al., 2010), and it was clear that texture differences often need to be larger for solids foods to impact on eating rate compared to liquid or semi-solid differences. In a follow up study, Forde and colleagues presented whole and pureed versions of the same lunch meal that produced a 20% decrease in eating rate (52g/min vs. 42g/min) and a significant decrease in energy intake for the whole meal (Forde et al., 2013b). Using a similar approach, a follow up study demonstrated that texture induced changes in eating rate led to a 13% (average 93kcals) reduction in energy intake at a lunchtime meal, with no subsequent compensation at the evening meal (Bolhuis et al., 2014). Eating rate analysis of the hard vs. soft meals agreed with earlier studies and showed a decrease in eating rate of approximately 20% led to the decrease in overall energy of 13%, (Figure 1, 2, 3). These effect sizes are comparable with the previous findings when eating rate had been manipulated through verbal instruction and reduced energy by 14.6%, 92kcals (Forde et al., 2013b), 16.5%, 71kcals (Scisco et al., 2011), 12.1%, 123kcals in men (Martin et al., 2007), 12% reduction (Smit et al., 2011) and 10.3%, 67kcals (Andrade et al., 2008). The consistency and effect size of interventions that manipulate eating rate through the textures consumed is striking and significantly larger than ingredient based approaches such as seen in satiety trials with added fibers or protein.

The implication is that participants in these trials seem to eat in response to the textures served, as in all cases subjects were instructed to eat in their normal way, eat until comfortably full and there were no differences in subjective appetite ratings recorded after the meal. Karl and colleagues manipulated both energy density and eating rate using verbal instructions, and found a synergistic interaction between eating rate and an energy density in producing a greater reduction in energy intake than either intervention separately (Karl et al., 2011). Interestingly, energy density and eating rate combine to reduce energy intake, but only eating rate influenced the volume of food consumed, perhaps suggesting an important role for the physical act of chewing and processing a food in the development of satiation within a meal. There is likely to be a significant contribution from cognitive expectations and learned associations between certain textures and eating behaviours and the ‘usual’ energy associated with their consumption, which could contributes to a person’s experience of consuming harder textured foods. For example, slower eating rates, longer oral duration times and higher chewiness are positively related to higher expectations of fullness and satiety across a range of savoury foods (Forde et al., 2013a). Food texture may cue the nutrient and energy content of the foods we consume through a combination of sensory characteristics (thick, hard, chewy), the eating behaviour (fast/slow eating rate, large bite/small bite) and learned associations with post-ingestive feelings of fullness. We are currently only at the beginning of our understanding of how sensory, physiological and cognitive cues interact in the development of satiation and inform the decision to continue or to stop eating during a meal.

Figure 1: Food intake at lunch of softer-textured and harder-textured foods, n = 50 (means + SD). Total is the sum of hamburger and rice salad in either soft or hard versions.
(From Bolhuis et al 2014, PLoS One)

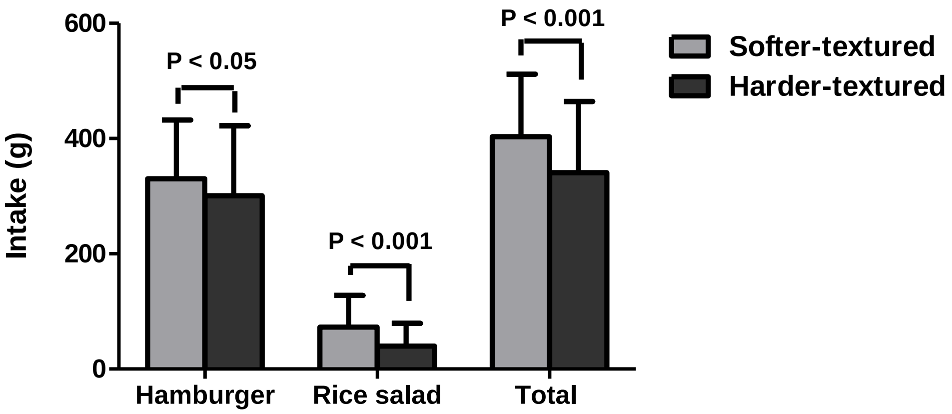


Figure: 2: Energy intake at lunch and dinner, n = 50 (means and SD)
(From Bolhuis et al 2014, PLoS One)

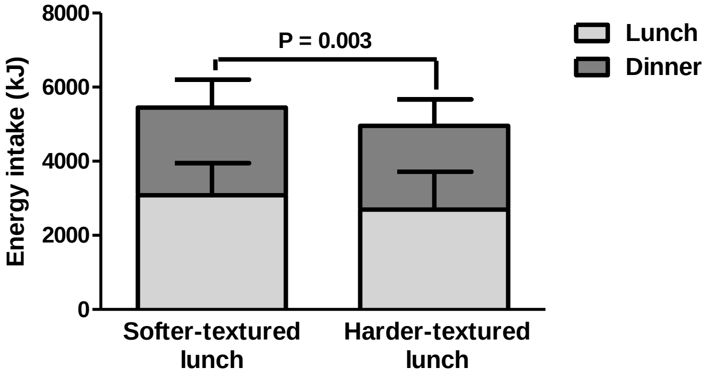
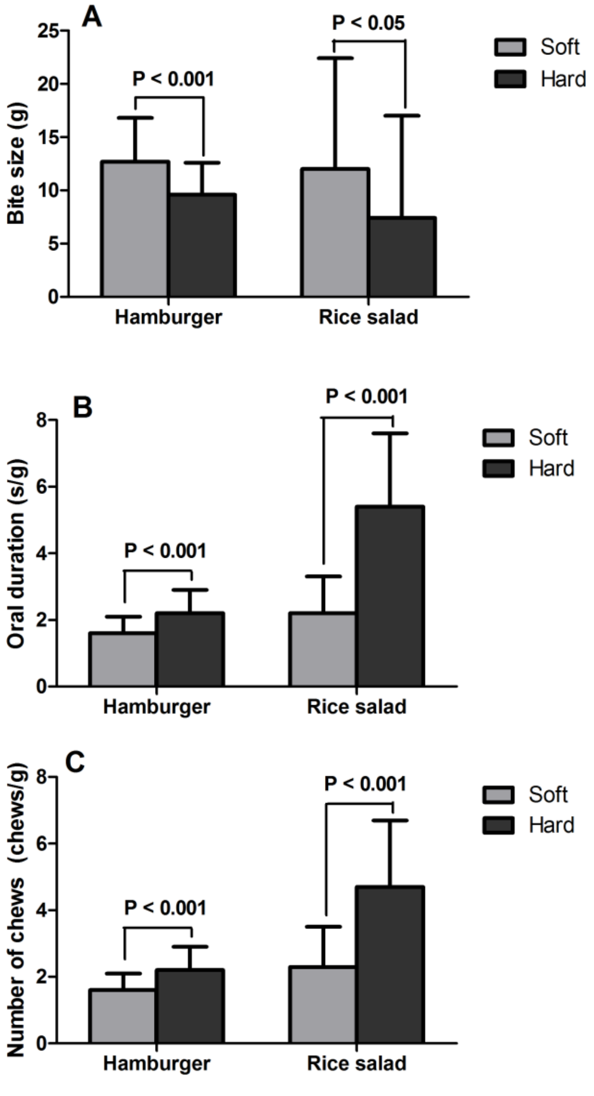


Figure 3: Differences in oral processing characteristics of soft and hard foods, n = 36 (means and SD); bite size (g) (A), oral residence duration (s/g) (B) and chews (no of chews/g) (C). *(From Bolhuis et al 2014, PLoS One)*



4.3: Sensory Enhanced Satiation: Combining Food Texture and Flavour to Enhance Fullness

The effect of food texture on eating rate and intake (satiation) is now well accepted and when compared to the relative influence of the other senses, seems to be much greater and more consistent. Few studies have attempted to combine texture and flavour cues to maximize the satiating properties of a food. Several studies have closely studied how beverage thickness (texture) and creaminess (flavour) interact to form our impression of fullness. Using a pre-load paradigm, Yeomans and Chambers were able to show better energy compensation when the sensory properties of a pre-load were aligned with the underlying energy content (Yeomans and Chambers, 2011). In a further study, when the creaminess and thickness of a beverage were gradually increased there was a parallel increase in the expected fullness anticipated on consumption (McCrickerd et al., 2012). Using the same beverage model, thicker and creamier versions of a beverage were selected and consumed in smaller quantities but when creaminess was changed without a thickness manipulation, the impact was much smaller (McCrickerd et al., 2014). This seems reasonable given the negligible impact of retro-nasal aroma on satiation (Ruijschop et al., 2009a) and the small comparative impact of taste on satiation (Bolhuis et al., 2011). The synergy between texture, taste and aroma cues in promoting fullness has been termed 'sensory enhanced satiety', where sensory cues can be used to enhance expectations and feelings of fullness when covertly reducing the overall energy content of a food (Chambers et al., 2015).

An important research challenge for the future will be to explore how best to optimize sensory and nutritional properties across a range of food types and to better understand the interplay between sensory enhancement and step-wise calorie reductions. At what energy content is adding additional thickness and creaminess no longer effective in enhancing feelings of fullness? To date most of the effects summarised above have been observed using acute feeding trials or preload designs, with only one study looking at energy compensation across the day (Bolhuis et al., 2014). To validate the efficacy of sensory approaches in sustaining energy reduction and satisfaction it is now necessary to explore whether these large and consistent effects are maintained with repeated exposure over time.

5.0: Conclusions and Future Perspectives: Using flavor to Design Reduced Calorie Foods

Sensory perception plays an important role in connecting the structural and chemical properties of foods to palatability and the foods underlying nutritional value. The sensory properties of a food or beverage act as powerful 'active ingredients' that functionally influences food intake behaviours far beyond simply motivating liking, stimulating and curtailing the desire to consume and enhancing the post-ingestive experiences imparted. Sensory properties can influence acute energy intake within and across meals, and inform the long-term regulation of energy intake through dietary learning. Through this, taste, smell and texture make an important contribution to the onset of satiation and the regulation of energy intake.

The emerging evidence presented in the current chapter highlights the importance of nutrient-taste congruency and the learned associations between taste, texture and eating behaviours. A deeper understanding of how food texture moderates eating rate and specific sensory properties cue the arrival of calories will make it possible to design foods that promote healthier habitual food intake decisions and eating behaviours. Weight loss and maintenance is achieved when the calories consumed are equal to or slightly less than the calories expended. Successful adherence to a calorie-restriction regime is extremely challenging and often unsuccessful as the best intentions in the world are no match for the drive to consume and enjoy food. Diets fail and new diets are born. When it comes to successful energy balance and healthy weight, a diet by any other name is still all about energy (Van Horn, 2014). Flavours can conceal covert manipulation of the energy content of foods and when these calorie reductions are judicious and realistic, calories can be successfully restricted without any associated feelings of hunger or deprivation. Minor changes to energy intake within the day can cumulatively result in sustained energy reductions and weight loss (Levitsky and Pacanowski, 2011). A promising direction for calorie reduction will be to modify food texture and flavour intensity in combination, to explore the extent to which calories can be successfully reduced without re-bound hunger or compensatory eating. Identifying a suitable 'calorie threshold' above which there is no re-bound hunger compensatory eating will enable a dilution of dietary energy density without the associated feelings of deprivation or restriction associated with dieting. Using the appropriate food textures to slow food intake we estimate that a 20% decrease in eating rate will decrease energy intake by approximately 10-15%, with no impact on subsequent feelings of hunger or fullness (Forde et al., 2013b, Bolhuis et al., 2014). In addition, a doubling of the oro-sensory exposure time has been shown to reduce ad-libitum food intake by 30-35%. These effects now need to be tested longitudinally to prove their longevity but the magnitude and consistency of these effects create the potential to optimise flavours and textures that compensate for missing calories and still deliver the full pleasure of eating.

There is now the opportunity for food manufacturers to reduce energy content and increase the satiating properties of products through using a range of sensory modifications to quality, intensity and texture (Chambers et al., 2015). A key feature of this new approach to enhancing the fullness of lower calorie foods is to optimize flavour intensities with food textures that slow eating rates and increase the duration of oro-sensory exposure to the calories ingested.

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