1 Introducing sensory and cognitive influences on satiation and satiety

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1.1 APPETITE CONTROL IN CONTEXT

The worldwide increase in incidence of overweight and obesity represents one of the biggest public health challenges of recent times. Statistics on obesity are startling: the proportion of the population in the United States who meet World Health Organisation (WHO) criteria for obesity have risen from around 7% in 1985 to 30% in 2015. In 2014, more than one in four people were obese in countries as diverse as New Zealand, Mexico, Canada, Hungary and Chile. The WHO estimated that by 2014 39% of the world’s population met the criteria for overweight, and 13% were obese, with more people overweight than malnourished for the first time in recorded history.

These statistics make understanding causes of weight gain an imperative. Weight gain is the consequence of storage of excess nutrients when there is an imbalance between energy intake and energy expenditure. Thus when intake of sources of energy in the diet, primarily fat and carbohydrate, exceeds short-term energy needs (the sum of basal metabolism, thermogenesis and energy needed for exercise and cognitive activity), the excess is stored. Most of the excess is converted to body fat, either directly by processing of ingested fat or through
conversion of excess carbohydrate into fat by the liver. However, excess intake arises only when factors that encourage short-term intake are not regulated by the systems involved in promoting energy expenditure and, crucially in the context of this book, inhibiting further food intake. It is noteworthy that despite the worldwide increase in obesity, many consumers maintain a stable weight. This implies that even in the modern obesogenic environment it is possible to maintain an appropriate balance between energy input and output, but that individual differences in sensitivity to external cues promoting intake and homeostatic processes regulating appetite make some individuals prone to over-consumption. Since humans typically eat at prescribed times dictated by cultural convention, it has been argued that understanding the processes that lead to suppression of appetite after a meal are key to understanding how altering the food environment may help promote individual appetite regulation [1–5].

1.2 SATIATION AND SATIETY: A BRIEF OVERVIEW

The modern interpretation of the terms “satiation” and “satiety” are most clearly encapsulated in the description of processes involved in appetite control commonly referred to as the “satiety cascade” [6]. In that descriptive model, satiation was defined as the processes that bring a meal to an end and satiety as the suppression of appetite post-ingestion. This specific interpretation of satiation and satiety is now widely accepted. The chapters in this book all examine aspects of two types of influence on satiation and satiety. The primary focus here is on how the sensory features of the foods and drinks we ingest influence the decisions that lead to meal termination (satiation) and also modify the processes that suppress appetite after ingestion (satiety). There are also chapters that highlight more cognitive elements that also modify both the interpretation of sensory cues and satiation and satiety more directly. Although models such as the satiety cascade fully recognised the importance of these cognitive and sensory influences, the majority of research on satiety remains focussed on physiological signals arising in the gut as a consequence of food ingestion. However, an understanding of these gut-derived signals is needed in order to put the main chapters in this volume into a broader context. The reader can find a more detailed
description and discussion of these gut-based satiety signals in one of a number of more detailed reviews [3,7–10].

The view of satiety most commonly described when discussing the role of gut-based satiety signals sees the gut effectively as a sensor that sends signals about the nutrients it can detect to the brain [3,11,12]. This gut-to-brain signalling is clearly a major component of the physiological basis of satiety experienced post-ingestion. However, what the present volume clearly demonstrates is that these gut-derived physiological signals are only part of the story and that both cognitive and sensory cues at the point of ingestion can clearly modify the way the body experiences satiety from the same set of nutrients depending on the context in which those nutrients were ingested. Thus understanding gut-derived physiological signals is an important component of satiety, but they can only be interpreted in the context of all signals relating to ingestion, including those arising from both the sensory experience of food and beliefs about the likely effects of that food on appetite.

What then are the principle gut-derived signals? Arguably the most important signals are specific peptides released in the gut in response to specific nutrient signals and whose purpose is to regulate the passage of food though the gut to optimise digestion and nutrient absorption. One key aspect of that control process is to modify ingestion to ensure an appropriate supply of nutrients, and it is likely that the gut-based satiety signals have evolved at least partly for that reason. The first such signal to be identified was cholecystokinin, first shown to modify ingestion in rats in 1973 [13], but since then many more gut-based signals have been identified, most of which appear to have roles in suppressing appetite (and are described as satiety signals), including glucagon-like peptide 1 (GLP1), polypeptide YY (PYY), oxyntomodulin (OXM) and pancreatic polypeptide (PP). A further gut-derived signal, ghrelin, has the opposite effect, increasing the experience of appetite in humans and increasing food intake in humans [14–17] and other species [18,19]: see Hussain and Bloom and Guyenet and Schwartz [12,20] for recent reviews. Thus ghrelin stands apart as the only gut-derived hormonal “hunger signal”.

The evidence supporting specific roles of these different gut signals in satiety typically involves a combination of studies in animals showing reduced food intake after administration of these compounds, evidence that such effects are consistent with a normal cessation of feeding rather than an indirect effect through malaise, and studies showing both reduced rated appetite and food intake in humans, again in the absence of any
confounding malaise: this evidence has been reviewed at length by many authors [3,7,10,21], and a full review is beyond the scope of this introduction. What the current volume does do, however, is put these physiological satiety cues into the broader context of other signals associated with food ingestion, particularly those derived from the sensory characteristics of foods and drinks.

1.3 SENSORY INFLUENCES ON SATIATION AND SATIETY: A BRIEF HISTORY

The chapters in this volume provide timely summaries of recent progress in understanding sensory and cognitive influences on satiation and satiety that build on ideas founded in classic studies in recent decades. Arguably the most influential concept during this time has been sensory specific satiety (SSS), and this concept is discussed from different perspectives in the chapters by Vickers (Chapter 2), De Graaf and Boesveldt (Chapter 3) and Piqueras Fiszman (Chapter 8). Sensory specific satiety is a concept founded in changes in liking for foods as a consequence of ingestion. The key observation is that liking for a food that is being consumed decreases, but liking for other foods which are not being consumed is maintained. The original observations came from studies in rats by the pioneering appetite researcher Jacques Le Magnen [22]: he observed that rats ate considerably more when provided with a variety of different-flavoured foods than when offered just a single food. The actual term SSS, however, came from seminal studies by Barbara and Edmund Rolls showing how rated liking for a consumed food decreased, but liking was unaltered for other non-consumed foods [23]. Although the change in liking occurs during ingestion and so may be better thought of as relating to satiation than satiety in our modern classification of appetite control, the term SSS has become such a clear label for this phenomenon that it remains. The key finding that there were neural correlates of SSS in the responses of single neurones in the lateral hypothalamus of monkeys [24] provided strong support for the idea that SSS is a key component of satiation and is often viewed as one of three key sensory or cognitive influences on meal size (the others being conditioned satiety and gustatory alliesthesia). SSS remains the most widely cited explanation for the role of variety in increasing food intake [25–28]. Given its importance in this context, SSS is an important element of this book.
Alliesthesia, or negative gustatory alliesthesia, to use its full name, was a concept introduced in 1968 by Michel Cabanac to discuss how liking for specific sensory characteristics of a food, most notably a sweet taste, was modified by homeostatic signals relating to internal state [29]. His fundamental argument was that liking for signals relating to energy, such as sweet taste, was greater when hungry than when sated [30], and Cabanac published extensively on this. (See Cabanac [31–33]). Although the term alliesthesia is used much less often by current researchers, key questions around the role of sweetness in satiety have become very important, and the role of sweetness in particular is consequently discussed in two chapters here: De Graaf and Boesveldt (Chapter 3) discuss sweetness more broadly from a perspective of sensory signals influencing appetite, while Hogenkamp (Chapter 4) asks more specifically the extent to which sweetness acts as a satiety signal, specifically focussing on the effects of low-energy sweeteners. Several recent developments make the issue of sweetness particularly relevant, most dramatically the claim that sugar may be addictive [34–36] and cause over-eating [37,38], and that as a consequence, several countries are introducing specific financial disincentives to dissuade over-consumption of sugar-sweetened beverages in particular (“sugar taxes”). Although the focus on sweetness has moved on from the early discussion of alliesthesia, sweetness rightly remains a critical area of discussion in relation to sensory influences on satiety.

Alliesthesia was founded in the homeostatic tradition which considered how expression of liking for foods was related to energetic needs. Since the concept of alliesthesia was developed, there has been increasing interest in the rewarding nature of eating. In its extreme form, an alliesthesia hedonic evaluation was seen, at least in part, as an expression of the need for a particular set of nutrients. However, an area that has changed markedly since the initial ideas of alliesthesia were developed is how we conceive food reward. In discussing the relationship between food reward and satiety, Temple (Chapter 5), reminds us that “our drive to eat results from the integration of central and peripheral physiological cues along with psychological input that can modify, modulate, and override these physiological signals”, building on what was discussed earlier in this brief introduction. What Temple adds to this volume is a timely discussion of the importance of the relative reinforcing value of food in this context. She notes how highly rewarding foods can override satiation to promote short-term over-consumption and then explores how
the concept of relative reinforcing value might predict the extent to which an individual may be prone to over-consumption and consequent weight gain, offering a potential mechanism to explain the individual differences in propensity to obesity discussed at the opening of this introduction. These ideas draw heavily on concepts drawn from broader motivated behaviours, including drug addiction, and in doing so help put the current work into a wider context of individual sensitivity to reward.

The third traditional cognitive/sensory theory relating to satiation was conditioned satiety, a phenomenon which again can be traced back to the work of Jacques Le Magnen [39]. However, the person whose work brought this concept to prominence was David Booth, who has written extensively on conditioned satiety [40–42]. In essence, the claim for conditioned satiety is that co-experience of a particular food with a mildly aversive gastric experience such as bloating leads to the sensory characteristic of that food acting to control the size of subsequent meals. Some of the clearest evidence for this came from studies of the meal size of rats switching from low- to high-protein diets [43]: initially meal size remained the same, but meal frequency was reduced (since the diets were more nutrient-dense); over a few days, meal size decreased, interpreted as the rats learning to reduce intake to avoid the unpleasant effects of over-satiation. Although Booth went on to report studies which were interpreted as supporting the conditioned satiety idea in humans [44,45], many subsequent studies have failed to find evidence that fits with the conditioned satiety hypothesis [46–48]. A recent review of all studies which explored conditioned satiety in humans found that only 25% of studies reporting positive findings [49]. It may be that in real life we rarely consume foods in a manner that creates the specific conditions that result in conditioned satiety.

However, it could be argued that the study of conditioned satiety was one of the drivers for recent interest in other sensory and cognitive influences on satiation and satiety, most notably the idea that the specific sensory characteristics of foods lead to measurable expectations about how ingestion of that food will alter appetite [50,51]. These expectations have been argued to arise through past associations between the sensory characteristics of foods and the actual post-ingestive experience of satiety [50]. For example, estimates of expected satiety are more closely related to actual nutrient content for familiar foods, where there would have been an opportunity to learn, than for less familiar foods [52]. The chapter by McCrickeerd (Chapter 6) draws on these recent ideas to
develop a model of satiety based on matching the expectations generated by sensory and cognitive cues at the point of ingestion to the actual experience of satiety after ingestion. These cognitive influences on satiety are clearly distinct from the very specific idea of conditioned satiety, but the core ideas can be seen as an extension of the premise that our real experience of the effects of foods on our appetite and satiety are key factors that shape the way we respond to the sight, smell and taste of food and so determine how much to consume.

### 1.4 NEW DIRECTIONS

The classic study of satiety has focussed on a relatively narrow set of ideas based on interactions between sensory cues and physiological effects of nutrients: these ideas have moved our understanding of satiety a long way. But arguably, the real innovation in this book is the inclusion of areas of research which fall outside the traditional areas of focus for satiety. When key ideas such as SSS, alliesthesia and conditioned satiety were being formed and tested, we understood that orosensory chemoreceptors allowed detection of just four basic tastes: sweet, sour, salty and bitter. Of these, only one appeared to have relevance to satiety (sweetness, as discussed by De Graaf and Boesveldt in Chapter 3). The more recent inclusion of umami as the recognised fifth taste opened up the possibility that there was a new taste component that could be related to satiety, an idea explored in brief by De Graaf and Boesveldt (Chapter 3) and then explored in much greater detail by Yeomans and Masic (Chapter 7). The principle argument here is relatively simple: when Kikunae Ikeda first proposed umami as a specific flavour component [53], he suggested that perhaps umami served as a cue to predict the presence of protein in food. Since protein is often described as the most satiating macro-nutrient [54–58], the idea then follows that perhaps umami taste itself impacts satiety, and Yeomans and Masic (Chapter 7) provide clear evidence that this is so.

But the sensory experience of food is based on much more than taste perception: as Piqueras Fiszman explains in detail in Chapter 8, our perception of flavour involves the multi-sensory integration of cues arising from olfaction, gustation and somatosensation experienced when food is placed in the mouth [59–62]. It thus follows that sensory cues other than taste influence satiety, and the chapter by De Graaf and
Boesveldt (Chapter 3) specifically explores the role of smell as well as taste in this context. However, as we have mentioned previously, the mere sight of a food can generate explicit satiety expectations (discussed by McCrickerd, Chapter 6). Piqueras Fiszman (Chapter 8) takes this further, exploring specifically how the colour and texture of food influence satiation and satiety, drawing on a diverse pool of evidence. The suggestion that texture plays a key role as a signal predicting likely nutrient content is a theme that emerges in many of these chapters and is an area ripe for further research. It is also an area where there is perhaps more potential for food manufacturers to use textural cues to increase satiety expectations when foods are consumed in order to increase the likelihood that consumers may better regulate their subsequent eating. A more applied angle is taken in the final chapter by Lett and Norton (Chapter 9), in which they discuss how the application of principles from chemical engineering can be used to manipulate the structure of products and thereby alter the satiating potential of these products.

1.5 CONCLUDING REMARKS

Sensory and cognitive influences on satiety are too frequently ignored. The focus of research into satiety on physiological and neural mechanisms has often ignored how consumer beliefs combined with sensory cues might help explain some of the great puzzles in satiety, such as why drinks generate weaker satiety whereas the same nutrients consumed in solid form can be very satiating. This book brings together a unique grouping of scientists from varied academic disciplines, including those approaching this issue from the perspective of sensory science, nutrition, food science, psychology and chemical engineering, to highlight many of the recent developments in the broad area of cognitive and sensory influences on satiation and satiety.

References
