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Apple versus chocolate: Evidence for discrimination of distension-related and calorie-related satiety signals in post-prandial fullness and hunger, and in the quality and location of other body sensations

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ABSTRACT

Gastric distension and detection of macronutrients (calories) in the gut are determinants of satiation and satiety. We tested effects of these variables on body sensations after eating, and their connection with visual-analogue scale (VAS) hunger and fullness ratings. Participants completed VAS ratings and quality and location of body sensations tasks after consumption of milk chocolate (38 g, 200 kcal) versus fresh apple fruit matched for weight (38 g, 20 kcal) and matched for calories (380 g, 200 kcal). Effects of food weight (380 vs 38 g) were large and located predominantly in the abdominal region. They also occupied a greater body area and occurred sooner after eating than effects related to calories (200 vs 20 kcal). The same pattern was apparent in the results from the quality of sensations task. VAS ratings indicated that hunger was affected by food volume and calories, whereas fullness was affected primarily by food volume. Together, these results provide evidence of dissociation of the perceived after-effects of food ingestion related to food volume and food calorie content in humans. Additionally, the studies demonstrate the utility of two rarely used, semi-quantitative tasks, which generate information on the identity, intensity, valence, and location of eating-related sensations.

1. Introduction

In many studies of human appetite control, participants are asked to make hunger and fullness ratings. As we have described elsewhere [1], these ratings tend to be highly negatively correlated, which is consistent with a relative lack of fullness (an 'empty stomach') being a major stimulus for appetite or desire to eat [2–4]. In everyday language we typically express this state as being 'hungry', even though only a few hours or less may have elapsed since our last meal and we are not significantly 'depleted' of fuel [2]. In turn, it is well-established that both gastric distension (via stretch and tension mechanoreception) and detection of macronutrients in the gut contribute to late meal and post-meal states of the inhibition of appetite (i.e., satiation and satiety) (e.g., [5–10]). The extent to which distension-related and calorie-related[1] signals contribute to satiety will presumably vary with food calorie density, with the distension signal being relatively more dominant for calorie-dilute foods and the calorie signal being relatively more dominant for calorie-dense foods [11].

Based on these considerations, the primary question we sought to answer in the present study was whether these signals give rise to discriminably different body sensations. To achieve this aim we measured the magnitude, location, time course and valence of body satiety-related sensations in participants after they had consumed an energy-dilute food (apple) and an energy dense food (chocolate). In addition to visual analogue scale (VAS) ratings of hunger and fullness [12], we used measures that built on methods developed in infrequently cited earlier studies [13–15]. These studies investigated body sensations accompanying primarily the imagined or actual experience of brief or longer periods of food deprivation, although some information was also collected on body sensations experienced during and after eating. For example, in the study by Friedman and colleagues [13], study participants recorded their body sensations during an actual 22 h fast, and immediately and 4 h after eating. We also used the thought-listing task, borrowed from cognitive psychology [16].

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[1] The presence of sugars, amino acids and fatty acids in the upper gastrointestinal tract triggers neuroendocrine signals that are major contributors to satiation and early post-prandial satiety [49,50]. Calorie-for-calorie, these nutrients vary somewhat in their satiating potency, however from the perspective of energy balance it is the overall energy content of a meal that matters [37].

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Apple and chocolate differ ten-fold in energy density, due largely to the difference in their water content. Importantly, however, a substantial amount water in fresh apple is contained within intact cells in the fruit [17], so it will contribute significantly to stomach distension. This contrasts with the same volume of water drunk with food, which empties rapidly from the stomach, due to the process of gastric sieving [18–20]. Consistent with this, consumption of water on its own has little effect on hunger and fullness (e.g., [21,22]).

We compared the effects of consuming 38 g (200 kcal) of chocolate on satiety-related body sensations with the effects of consuming amounts of fresh apple matched with the chocolate for calories (380 g, 200 kcal), and for weight (38 g, 20 kcal). We conducted a preliminary study on imagined consumption of apple and chocolate to pilot our measures and to estimate effects sizes. The results of this preliminary study (described in supplementary materials) indicated that together the various measures should be able to distinguish between distension (380 g apple versus 38 g chocolate) and calorie (38 g chocolate versus 38 g apple) effects.

Specifically, we hypothesised differences in effects on fullness versus effects on hunger, based on the possibility that food volume primarily drives fullness, and food calorie content primarily affects hunger. Because there is lag phase in the gastric emptying of solid meals (e.g., [23]), and distension and calories seemingly act synergistically to inhibit appetite (e.g., [6]), we also hypothesised that the effects of calories would be delayed compared with the effects of food volume. Therefore, we applied all our measures immediately, and 10, 60 and 120 min after food consumption. However, for two reasons we focused our analyses on the 60 min timepoint. First, this was because previous studies have demonstrated reliable effects of calorie manipulations on appetite 60 min post ingestion, as measured by hunger and fullness VAS ratings and test-meal energy intake (e.g., [24–26]). And second, because the results of our preliminary study suggested that effects of distension persist for at least 60 min after the consumption of a relatively large volume of food (380 g apples). Additionally, we included the 120 min timepoint to test for the potential longevity of effects.

2. Methods

2.1. Overview

In a within-subjects design, 3 h after breakfast participants consumed, on separate days, 380 g apple, 38 g chocolate and 38 g apple. Immediately, 10 min, 1 h and 2 h after finishing eating the portion of apple or chocolate, they completed three tasks measuring the identity, intensity, quality and location of satiety-related sensations.

2.2. Participants

The effect sizes observed in the preliminary study were very large. For example, Cohen's d_{av} [27] for the difference in VAS hunger after eating apple and chocolate was 1.96, and for the difference in VAS fullness it was 1.59. Even assuming zero correlation between the sets of measurements, a sample size of $n < 6$ is needed to obtain 95% power to detect effect sizes of these magnitudes at alpha = 0.05 (2-tail) [28]. Accordingly, six participants (3 women and 3 men) were recruited for the study. Participants were recruited via social media and word of mouth. They were of varied ethnic backgrounds, but all were fluent English language speakers. Their mean age was 33 years (range 22–60 years). Five participants were of healthy weight, whilst there was one participant with overweight. They were low to moderately active individuals (mean ± SD physical activity score of 32 ± 13, self-rated on a 0–100 point visual-analogue scale, anchored 'sedentary' to 'very physically active').

The procedures for this study, and the preliminary study, were approved by the University of Bristol, Faculty of Science Human Research Ethics Committee (approval code: 070313FSSOP). Informed consent for participation in the studies was obtained from all participants via a written or electronic document.

2.3. Design

The study was conducted according to a within-subjects design. Participants completed satiety-related measures following consumption, on consecutive days, of 380 g apple (200 kcal), 38 g milk chocolate (200 kcal) and 38 g apple (20 kcal). The order in which these foods were tested was fully counterbalanced across participants.

2.4. Materials

The foods were fresh Red Delicious apple and ION milk chocolate (ION S.A., Piraeus, Greece). The apple was served as either twenty (380 g portion) or two (38 g portion) approximately equal-sized, wedge-shaped pieces, with the core and stalk removed. 380 g is the weight of 2–3 medium-sized apples. The chocolate was served as two, equal-sized squares (38 g portion).

We created an e-document in Microsoft Word which contained step-by-step instructions for the test session, together with response pages on which the participants recorded their responses (e.g., by typing the words they generated in the quality of body sensations task, or using the Microsoft Word shapes tool (circle shape) to complete the location of body sensations task). The study was described in this document as the 'Apple and chocolate study'.

2.5. Measures

2.5.1. Task 1: quality of body sensations task

This task was based loosely on the thought-listing procedure reviewed by Cacioppo and colleagues [16]. We used a similar task successfully in previous research on attitudes and appetite in relation to eating chocolate [29]. Participants were instructed to (apple example) 'Please consider carefully what sensations you would feel in your body as a result of eating the apple pieces, and then write down in the box below as many single words or short phrases as you can to describe those sensations.' No time limit was placed on this activity. Next, participants were instructed to rate 'the pleasantness of each of the sensations you have listed, on a scale from −2 to +2, where −2 = very unpleasant, −1 = unpleasant, 0 = neutral, +1 = pleasant, and + 2 = very pleasant'. This procedure was designed to access words that participants choose spontaneously to describe the after-effects of eating, and to record the valence they assign to each of those words. For analysis, synonymous words (e.g., 'full' and 'fullness') were merged into a single category, and mean valence assigned to those synonymous words was calculated. The term 'quality of body sensations' task therefore refers collectively to the identity of the sensation or feeling (fullness, nausea, sweetness, etc.) and to its valence (positive, neutral and negative).

2.5.2. Task 2: location of body sensations task

This task was very similar to that described by Friedman and colleagues [13]. Participants were presented with a sex-neutral outline of a human figure (as shown in Fig. 1, with results added), scaled to 15.3 cm tall on an A4-size page below the instruction: 'On the figure below, circle the place(s) in your body where you feel the effects of the apple pieces you have just finished eating. With your circle(s) show the size of the place(s) affected. Mark with a cross the place exactly where you feel the strongest effect.' (Apple, immediately after eating timepoint example.)

2.5.3. Task 3: visual analogue scales

The final task completed by participants comprised eight, 100-point, visual-analogue scales (VAS) (e.g., [1,12]). The instruction was: 'Please answer the following questions about how you feel by drawing a short vertical line at the appropriate point through each horizontal line.' The scales were labelled: 'I feel HUNGRY', and 'I feel FULL'.

2.6. Procedure

Participants were sent an information sheet to enable them to make a final, informed decision as to whether to participate in the study. The information sheet was titled 'Body sensations after food consumption', and it provided an outline description of the study procedures but gave no obvious clues as to the research hypotheses.

The study was conducted during COVID-19 lockdown. Participants were tested individually in their own home, supervised by the Experimenter (A.M.) via a Skype videocall. Each test session began at 11 am, 3 h after the participant had eaten their usual breakfast. The participant was seated in a room with minimal distraction. The food (i.e., apple or chocolate) was prepared and served to the participant on a white plate by a housemate (a relative or friend), according to instructions provided earlier. The time taken to consume the food was recorded covertly by the Experimenter. The Experimenter only answered procedural questions, for example about when to move on to the next task. The participant's responses on the various tasks were not visible to the Experimenter during the test session. The tasks were completed in the order described above (Sections 2.5.1 – 2.5.3), immediately, 10 min, 1 h and 2 h after eating the food. Participants also completed the hunger and fullness VAS ratings task shortly before the food was served. During breaks between tasks, participants engaged in normal, non-intensive activities. They were asked to neither eat nor drink anything further, except for a small amount of water if desired. The test session lasted approximately 2¼ hours in total. The participant's final task was to save the completed response document and email it to the Experimenter. Each participant completed their three test sessions (each in a different order) on consecutive days.

On completion of the study the participants were informed about the full purpose of the study, and they were thanked for contributing to our research.

It is worth noting that the method of testing participants remotely via a videocall functioned successfully. An advantage was that the Experimenter was able to supervise the participant in the familiar environment of each participant's own home, rather than requiring them to travel to be tested in an unfamiliar laboratory environment. Arguably, compared with laboratory-based studies, the method of testing we used (out of necessity) has the advantage of generating data more relevant to everyday life settings (i.e., it has greater ecological validity). Furthermore, home testing is more convenient and accessible for participants.

2.7. Data analysis

We tabulated and summarised the frequencies and calculated the mean valences of the different words generated in the quality of body sensations task, separately for the three food conditions at each timepoint.

For the location of body sensations task, we measured in mm the x and y coordinates of the centre point and the diameter of the area(s) circled by participants on the human figure outline (sized at 15.3 cm tall), from which we made visual representations of the group data for each food at each time interval using amCharts 5. This entailed superimposing the images from all participants. To avoid saturation of the images, the opacity of the 'strongest effect' (that each participant marked with a cross) at each time interval was weighted 0.2, and other sensations were weighted 0.06. Therefore, in the resulting group figure outline pictures, darker areas represent greater consensus of a sensation experienced at that location.

We also conducted quantitative analysis of the location of body sensations task area data (i.e., the sum of the areas marked by each participant for each food at each time interval) using a 2-way repeated measures ANOVA to test the effects of Food (380 g apple, 38 g chocolate and 38 g apple) and Time (task completed immediately, 10 min, 1 h and 2 h after eating). Similarly, we conducted a 2-way repeated measures ANOVA to test the effects of Food and Time on the VAS hunger and fullness ratings data (after eating minus before eating ratings). Finally, we followed up these analyses by conducting paired comparisons between the effects of the three food conditions at the 60 min time interval. The statistical analyses were carried out using IBM SPSS 28.0.0.0.

3. Results

3.1. Quality of body sensations task

The words and phrases that participants generated spontaneously to describe body sensations related to fullness and hunger after eating are listed in Table 1, together with the number of occurrences of each of those words and phrases. The overall number (grand total) of fullness-related words generated was substantially larger after consumption of 380 g of apple compared with either 38 g of chocolate or 38 g apple. In contrast, the number of hunger-related words generated was greatest after consumption of 38 g of apple (20 kcal), with little difference between the number of hunger-related words generated after consumption of 380 g of apple versus consumption of 38 g of chocolate (both

Table 1
Results for the quality of body sensations task, showing the number of fullness- and hunger-related words generated for each food condition at each time interval[a]

Time after eating	Fullness-related words Food consumed 380 g apple	38 g chocolate	38 g apple	Hunger-related words Food consumed 380 g apple	38 g chocolate	38 g apple
1 minute	Full (4) Stuffed (3) Bloated (2) Nauseous (1) Stomach distension (1) Stomach pain (1)		Bloated(2) Stuffed(1)		Hungry (2)	Hungry (1)
	Total (12)	**Total (0)**	**Total (3)**	**Total (0)**	**Total (2)**	**Total (1)**
10 minutes	Stuffed (4) Full (3) Bloated(1)	Bloated (2)	Stuffed (1)		Want more chocolate (1)	Hungry (3) Cravings (1)
	Total (8)	**Total (2)**	**Total (1)**	**Total (0)**	**Total (1)**	**Total (4)**
1 hour	Full (6)	Bloated (1) Full (1)	Bloated (1) Full (1)		Hungry (2)	Hungry (4) Cravings (1)
	Total (6)	**Total (2)**	**Total (2)**	**Total (0)**	**Total (2)**	**Total (5)**
2 hours	Full (1)	Bloated (2)		Hungry (4)	Hungry (1)	Hungry (4)
	Total (1)	**Total (2)**	**Total (0)**	**Total (4)**	**Total (1)**	**Total (4)**
	Grand total (27)	**Grand total (6)**	**Grand total (6)**	**Grand total (4)**	**Grand total (6)**	**Grand total (14)**

[a] A full list of the words generated, together with their assigned valence, is presented in Supplementary Materials Table S1. Number of occurrences of each word are shown in brackets.

containing 200 kcals). The pattern of results at one hour after eating was similar to this overall pattern: that is, fullness covaried with the weight of food consumed and hunger covaried more with the energy content of the food consumed. Furthermore, most of the words related to fullness were generated 1 and 10 min after consumption of the largest volume of food (380 g apple).

Mean valence (rated on a + 2 to −2 scale) assigned to fullness-related words was −0.51. The valence assigned to the word 'full' itself, however, was weakly positive (mean = 0.27), whereas the valence assigned, for example, to the words 'stuffed' (−1.33) and 'bloated' (−1.36), was substantially negative. The mean valence assigned to hunger-related words was −0.42. Valence assigned to these words did not vary obviously with food consumed or time interval.

Fuller details of the words generated in this task, together with their assigned valence, are presented in Supplementary Materials Table S1.

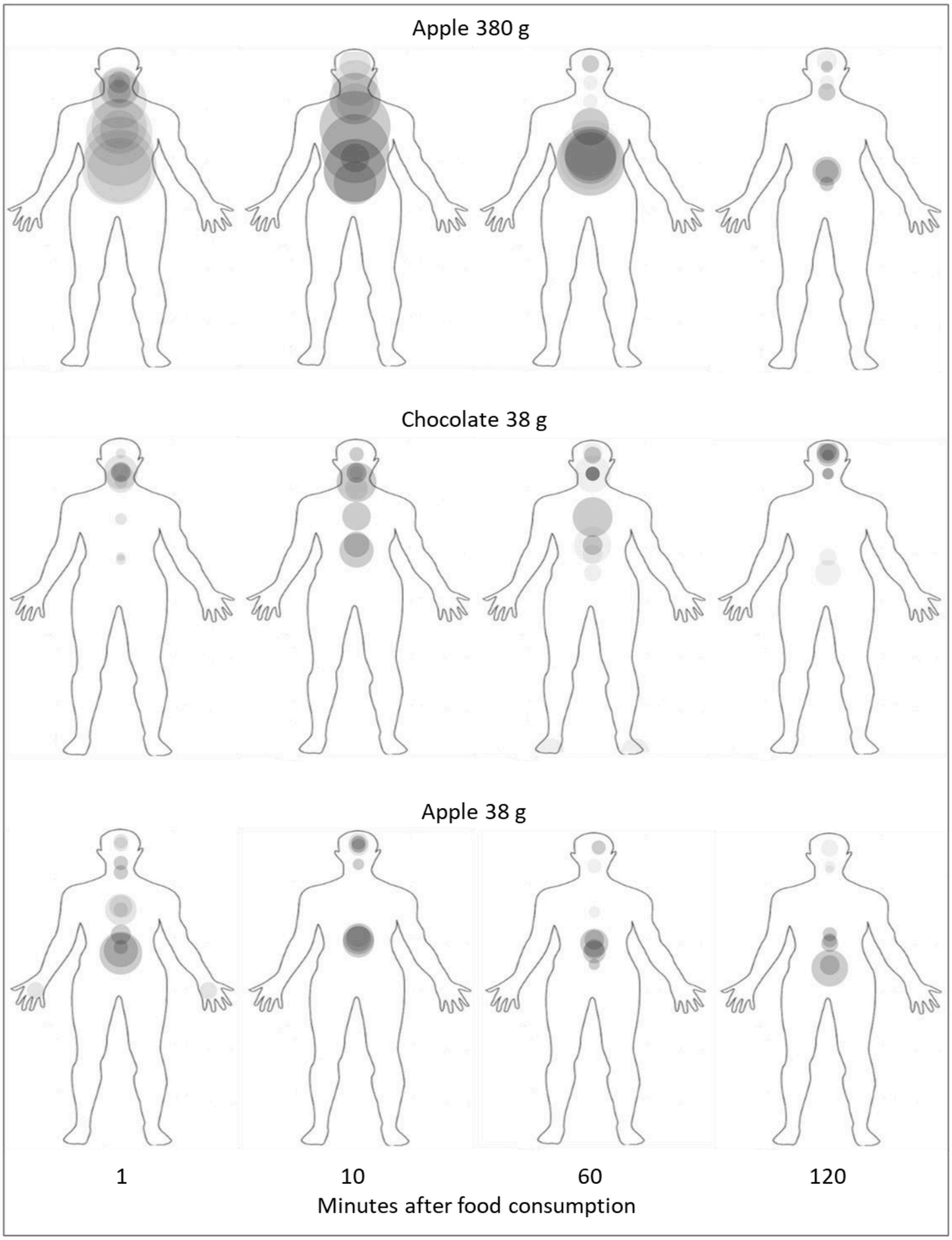

Fig. 1. Location and extent of body sensations indicated by participants 1 min (immediately), 10 min, 1 h and 2 h after consumption on separate days of 380 g of apple (200 kcal), 38 g of milk chocolate (200 kcal) and 38 g of apple (20 kcal). The circles represent the location and extent of where in their body participants felt the effects of eating the different foods at the four post-prandial intervals. Each picture was made by superimposing the drawings from six participants, as described in Section 2.7.

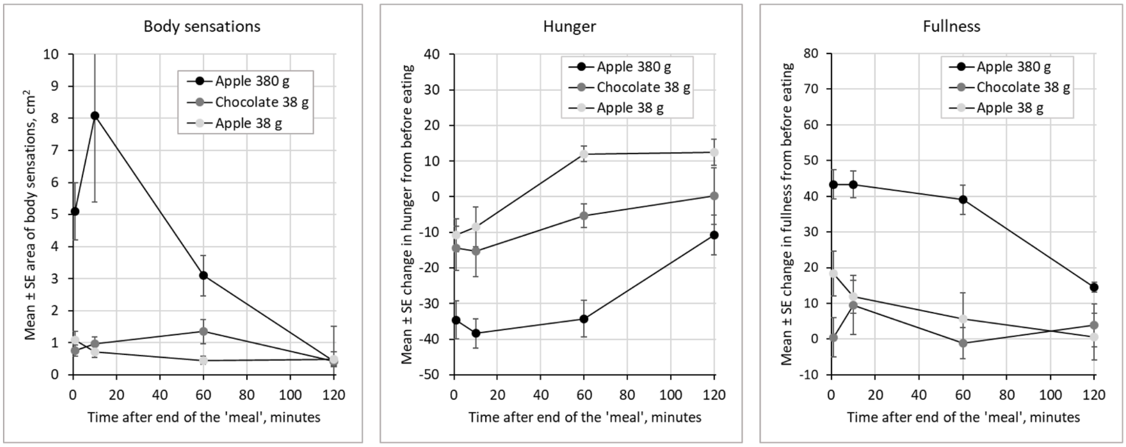

Fig. 2. Quantification of the extent of body sensations, and 0–100 point VAS hunger and fullness at four intervals after consumption on separate days of 380 g of apple (200 kcal), 38 g of chocolate of milk chocolate (200 kcal) and 38 g of apple (20 kcal).

3.2. Location of body sensations task

Fig. 1 shows the location and extent (size of area affected) of body sensations resulting from consumption of the foods. For the consumption of 380 g of apple, sensations were predominantly located in the mid and lower abdominal areas, but with sensations also reported in upper abdomen, throat and mouth at 1 and 10 min after food consumption. Mid and lower abdominal sensations were reported after consumption of 38 g of apple, but these covered a much smaller area than reported after consumption of 380 g of apple. A similarly small area of sensations was reported for the consumption of 38 g of chocolate, but the location for these sensations differed, being more focused in the areas of the upper abdomen, mouth, throat and head.

Quantification of the total area affected for each food and each time interval after consumption is shown in the left-hand panel of Fig. 2. This confirmed an effect of Food $F(2,10) = 17.24$, $p = 0.001$, $\eta p^2 = 0.775$, of Time ($F(3,15) = 5.75$, $p = 0.008$, $\eta p^2 = 0.535$, and a Food by Time interaction effect ($F(6,30) = 19.51$, $p = 0.001$, $\eta p^2 = 0.501$). The paired comparisons (paired *t*-tests) at one hour after food consumption revealed a difference between 380 g apple versus 38 g apple ($p = 0.010$), a difference between 380 g apple versus 38 g chocolate ($p = 0.045$), and a difference between 38 g apple versus 38 g chocolate ($p = 0.029$).

3.3. Visual analogue scale hunger and fullness ratings

The results for the VAS ratings of hunger and fullness are shown in the middle and right-hand panels of Fig. 2. Hunger and fullness mostly showed an inverse pattern of effects of food and time, except for the effect of consumption of 38 g of chocolate (200 kcal) versus consumption of 38 g of apple (20 kcal). These two 38 g food portions did not differ much in their effects on fullness, but hunger was higher after 38 g of apple than after 38 g of chocolate. Consumption of 380 g of apple had the largest effect on both hunger and fullness.

The statistical analysis confirmed an effect of Food $F(2,10) = 17.00$, $p = 0.001$, $\eta p^2 = 0.773$, and an effect of Time ($F(3,15) = 41.44$, $p < 0.0001$, $\eta p^2 = 0.892$ on hunger. There was not a Food by Time interaction effect ($F(6,30) = 1.36$, $p = 0.264$, $\eta p^2 = 0.213$) for hunger. It confirmed an effect of Food $F(2,10) = 13.17$, $p = 0.002$, $\eta p^2 = 0.725$, an effect of Time ($F(3,15) = 14.49$, $p = 0.0001$, $\eta p^2 = 0.743$, and a Food by Time interaction effect ($F(6,30) = 5.02$, $p = 0.001$, $\eta p^2 = 0.501$) for fullness. The paired comparisons (paired *t*-tests) at one hour after food consumption for hunger, revealed a difference between 380 g apple versus 38 g apple ($p = 0.0004$), a difference between 380 g apple versus 38 g chocolate ($p = 0.011$), and a difference between 38 g apple versus 38 g chocolate ($p = 0.009$). The paired comparisons at one hour after food consumption for fullness revealed a difference between 380 g apple versus 38 g apple ($p = 0.008$), a difference between 380 g apple versus 38 g chocolate ($p = 0.001$), but no difference between 38 g apple versus 38 g chocolate ($p = 0.493$).

3.4. Eating time

The time taken to eat 380 g apple (24.8 ± 2.7 mins) was greater than the time taken to eat either 38 g chocolate (7.3 ± 2.2 mins) or 38 g apple (6.2 ± 0.9 mins) ($p < 0.0001$, paired *t*-tests). The time taken to eat the 38 g food portions did not differ ($p = 0.549$).

4. Discussion

The effects of gastric distension and calories on satiety (and food reward) and their underlying physiological mechanisms have been studied extensively in non-human animals [e.g., [8–10,30,31]), but much less research has been done to directly contrast these effects of food ingestion in humans. The design of the present study, together with the three measurement tasks, demonstrated a dissociation of effects experienced by humans in relation to food volume and food calorie content.

The effects of food volume (380 g apple versus 38 g chocolate or 38 g apple) were clearly evident in all three tasks, including differences in the number of fullness-related words produced in the quality of body sensations task, and differences in the area occupied by sensations reported in the location of body sensations task. The comparison between 38 g of chocolate and 38 g of apple showed differences in the location of body sensations throughout the two hours after eating (Fig. 1). At least in part, this may be due to the different taste and texture of these foods, for example a lingering taste of chocolate, including its sweetness, in the mouth after consumption, compared with shorter-lasting sensations related to the crispness and high water content of apple. However, it is also possible that the location of sensations in the head, mouth, throat and upper abdomen after eating chocolate reflect an effect of calories; in contrast to the effect of volume felt primarily in the abdomen, initially in the upper abdomen and subsequently descending to the lower abdomen.

Oral exposure can contribute to satiety (e.g., [32–34]). That being so, the longer eating time (oral exposure time) for 380 g apple may account in part for its large effects, although it is noticeable that there was little difference between the apple conditions in area of sensations reported in the throat, mouth and head at 1 and 2 h after eating (Fig. 1). It is also the case that there were no substantial differences in hunger and fullness between the three conditions at the 2 h timepoint (Fig. 2), indicating too that participants were equally ready to eat again irrespective of the volume or calorie content of the food they had consumed 2 h previously (cf. [2,35]).

The early post-prandial effects of consuming apple versus chocolate on VAS hunger and fullness ratings appear to be driven by food volume, with the magnitude of the effects on the two scales being similar. In contrast, the VAS ratings completed at 1 h and 2 h after eating suggest different effects of volume and calories (Fig. 2). Specifically, 1 h after eating, fullness was higher in the large volume condition (380 g apple) compared with both of the low volume conditions, but fullness did not differ between the two low volume conditions (i.e., 38 g chocolate = 38 g apple) at this timepoint, or indeed at the other timepoints. In contrast, 1 h after eating, hunger differed between all three conditions (38 g apple > 38 g chocolate > 380 g apple), as did the area of body sensations reported (38 g apple < 38 g chocolate < 380 g apple). Together, these results, which we at least partly hypothesised, can be interpreted as an effect of volume, via gastric distension, on fullness, and a combined effect of volume and calories on hunger. This dissociation between the effects of food volume and calories is even supported by the patterns of spontaneous reports of hunger and fullness across conditions 1 h after eating (quality of body sensations task, Table 1).

Previously, we noted that there is often a strong inverse correlation between VAS hunger and fullness ratings (e.g., $r = -0.86$, [1]; and see also [12]), whereas this study demonstrates a partial dissociation of hunger and fullness. One reason for the dissociation may lie in the body cues that participants attend to when making judgments of their hunger and fullness. When asked to rate 'how full does your stomach feel' (rather than 'how full do you feel'), the correlation with hunger is smaller (e.g., $r = -0.44$, [1]). Although the fullness question in the present study was labelled simply 'I feel full', and the hunger question 'I feel hungry' (both anchored 'not at all' to 'extremely'), it is possible that completing the previous tasks, which required participants to spontaneously generate words to describe their feelings after food consumption and to record the body location and extent of those of feelings, facilitated discrimination between fullness and hunger.

Another example of the dissociation of hunger and fullness is that inflation of an intra-gastric balloon was found to increase fullness without having an appreciable effect on hunger [36]. The upper part of the balloon was placed 2 cm below the gastro-oesophageal junction, and it was inflated with 500 ml of warm water. Only the increase in fullness (Cohen's $d_{av} = 0.78$) was statistically significant, with much smaller decreases in hunger (Cohen's $d_{av} = 0.16$) and desire for food (Cohen's $d_{av} = 0.25$), and a small increase in discomfort (Cohen's $d_{av} = 0.31$) (effect sizes calculated as described by Lakens [37] from the data provided by Wang and colleagues [36] in their Fig. 2). In an earlier study, inflation of a gastric balloon was found to affect both hunger and fullness, however in that study there was also a significant increase in discomfort, possibly because of a higher mean volume of balloon inflation [38]. It does appear, therefore, that at least a moderate degree of gastric distension is felt as fullness, without greatly affecting hunger. That being so, it is understandable, notwithstanding the technical and clinical challenges, that the chronic implantation and inflation (to 300 or 400 ml) of a gastric balloon failed to bring about clinically significant weight loss in patients with obesity [39].

A hypothesis that follows from our proposal that hunger is affected by food volume and calories, whereas fullness is affected primarily by food volume, is that increasing the calorie content of a foodstuff without increasing its volume will decrease hunger but will not increase fullness. In partial support of this hypothesis, we found that consumption of a glucose-sweetened yogurt [25] or a glucose-sweetened drink [22] compared with the same volume of yogurt or drink sweetened with low-calorie sweeteners decreased hunger somewhat more that it increased fullness. The calorie differences in the yogurt and drink studies were 164 kcal and 188 kcal, respectively. On the other hand, Wardle [26], for example, found that manipulating the calorie content of orange juice by adding soluble starch (300 kcal versus 50 kcal drinks), affected hunger and fullness to a very similar extent. This suggests that the (English) word fullness, does also readily express the reduction in appetite caused by ingestion of calories, even though gastric distension is felt separately and is expressed separately as having a full stomach and, after eating a large volume of food, as feeling, for example, 'bloated' or 'stuffed'.

It is worth noting that labelling body sensations as hunger and/or fullness rests on explicit knowledge of recent eating. For example, individuals with amnesia fail to show reduced hunger or increased fullness after a meal despite reporting abdominal discomfort [40,41]. Furthermore, hunger was reduced more by intra-gastric infusion of soup when participants (without amnesia) were told that the infusate was tomato soup compared with when they were told it consisted of a 'nutrient or non-nutrient solution' [42]. Usually, though, it would seem to be relatively straightforward to locate and label sensations related to gastric distension, in that finishing a meal that swells the stomach is accompanied by a degree of discomfort, together with tightening and even visible swelling of the abdomen. In contrast, as discussed above, the effects of calories (38 g chocolate versus 38 g apple) identified in this study were associated with sensations referenced to predominantly outside the abdominal area (Fig. 1).

Whilst throughout this paper we refer to the 'effects of calories' (versus effects of food volume), it is important to be clear that it is the detection of macronutrients, primarily in the gut, rather than detection of calories per se, that contributes to satiation and satiety [2,37]. Post-absorptive sensing of, for example, glucose may also influence appetite, although the effects of hyperglycaemia on hunger, fullness and food intake appear to be modest [37,43]. These considerations are relevant to the current study because the chocolate and apple differed both in energy density and macronutrient composition. Specifically, in relation to the 'calorie effect' on hunger (Fig. 2, middle panel), the 38 g portions of chocolate and apple differed substantially both in their carbohydrate content (21 g vs 4.4 g) and their fat content (12 g vs 0.1 g). The 'calorie effect', therefore, is underpinned at least in part by independent effects of these macronutrients. Critically, though, as we note in footnote 1, the current consensus is that, calorie-for-calorie, the macronutrients do not differ appreciably in their satiating capacity [37], so it is reasonable to summarise the effects of energy density that we observed as 'effects of calories'.

Lastly, returning to our finding of a dissociation between hunger and fullness, there is separate evidence showing that during a meal gastrointestinal detection of calories generates separate satiation and reward signals (e.g., [30,31,44,45]). The calorie reward signal motivates eating in the moment and supports flavour nutrient learning (e.g., [30,31,44,45]), whereas it appears that neither gastric nor intestinal distension per se is intrinsically rewarding, but instead potentially aversive (e.g., [31,38,46]). We have shown, however, that fullness, together with meal enjoyment (which is a measure of food reward experienced during the meal), does contribute to eating satisfaction [47]. Our explanation of this finding is that we (humans) value the feeling of a full stomach because of the desire not to be distracted by the urge to eat between meals. Thus, the desire to feel satisfied is an extrinsic motive to include relatively bulky (energy dilute) foods in our diet. In support of this, in the present studies, the word 'full' was assigned weak positive valence, whereas the word 'stuffed' and 'bloated' were mostly assigned strong negative valence. Together, this suggests that the greatest satisfaction is felt when eating enjoyment is high and postprandial fullness is moderate to high, but not uncomfortable, and perhaps with tolerance of discomfort varying with the nature of post-prandial activities (e.g., resting versus working) [2].

In conclusion, the after-effects of eating related to food volume and calories are dissociable in both body location and quality of experience, with the satiating effects of volume also being manifest sooner than the effects of calories. Within this perspective, the decrease in hunger during a meal and its subsequent rise during the post-prandial interval would represent the integration of increasing and then decreasing volume and calorie satiation/satiety signals. Fullness largely varies inversely with hunger, although it appears to be more closely associated with the volume of food consumed (via gastric distention), especially if the question is 'how full is your stomach' [1]. Elsewhere, we have argued that, in the absence of knowing what there is to eat, a major determinant of appetite (or by another name, anticipated food reward) is the time elapsed since the previous meal and the size of that meal [1–4], which correlates inversely with the inhibitory effects of the presence of food in the gastro-intestinal tract. In everyday (English) language this is typically expressed in terms of how 'hungry' people say they feel.

Finally, it is worth reiterating that the quality of body sensations task and the location of body sensations task used in this study have been used only rarely in previous research on human eating behaviour; nevertheless, they show promise in generating new insights into the effects of the composition of foodstuffs on appetite. Whilst, testing the effects of 'real' foods, such as apple and chocolate, has the advantage of ecological validity, a next step might be to apply these measures together with the independent and, if feasible, disguised manipulation of the calorie content and volume of food consumed. These manipulations and measures could also have utility for investigating relevant individual differences, such as BMI, interoceptive awareness and disordered eating, or in studies related to, for example, mindful eating [48].

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Institutional review board statement

The research described in this paper involved human participants. The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the University of Bristol, Faculty of Science Human Research Ethics Committee (approval code 070313FSSOP, date of approval 10th June 2019).

Informed consent

Informed consent was obtained from all participants involved in the study.

Data

Full data generated from the quality of body sensations task are contained in the supplementary materials. Other data are available from the corresponding author on request.

CRediT authorship contribution statement

Anna Mantzavinou: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Peter J. Rogers:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Supervision, Visualization, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no conflict of interests in relation to this research.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.physbeh.2022.114051.

References

[1] P.J. Rogers, C.A. Hardman, Food reward. What it is and how to measure it, Appetite 90 (2015) 1–15, https://doi.org/10.1016/j.appet.2015.02.032.
[2] P.J. Rogers, J.M. Brunstrom, Appetite and energy balancing, Physiol. Behav. 164 (2016) 465–471, https://doi.org/10.1016/j.physbeh.2016.03.038.
[3] J.M. de Castro, Physiological, environmental, and subjective determinants of food Intake in humans: a meal pattern analysis, Physiol. Behav. 44 (1988) 651–659, https://doi.org/10.1016/0031-9384(88)90331-9.
[4] E.M. Stricker, Biological bases of hunger and satiety; therapeutic implications, Nutr. Rev. 42 (1984) 333–340, https://doi.org/10.1111/j.1753-4887.1984.tb02249.x.
[5] E.K. Williams, R.B. Chang, D.E. Strochlic, B.D. Umans, B.B. Lowell, S.D. Liberles, Sensory neurons that detect stretch and nutrients in the digestive system, Cell 166 (2016) 209–221, https://doi.org/10.1016/j.cell.2016.05.011.
[6] R.E. Steinert, A.C. Meyer-Gerspach, C. Beglinger, The role of the stomach in the control of appetite and the secretion of satiation peptides, Am. J. Physiol. Endocrinol. Metab. 302 (2012) E666–E673, https://doi.org/10.1152/ajpendo.00457.2011.
[7] P. Janssen, P. Vanden Berghe, S. Verschueren, A. Lehmann, I. Depoortere, J. Tack, Review article: the role of gastric motility in the control of food intake, Aliment. Pharmacol. Ther. 33 (2011) 880–894, https://doi.org/10.1111/j.1365-2036.2011.04609.x.
[8] T.L. Powley, R.J. Philips, Gastric satiation is volumetric, intestinal satiation is nutritive, Physiol. Behav. 82 (2004) 69–74, https://doi.org/10.1016/j.physbeh.2004.04.037.
[9] S.C. Woods, Gastrointestinal satiety signals I. An overview of gastrointestinal signals that influence food intake, Am. J. Physiol. Gastrointest. Liver Physiol. 286 (2004) G7–G13, https://doi.org/10.1152/ajpgi.00448.2003.
[10] G.P. Smith, Satiation: From Gut to Brain, Oxford University Press, New York NY, 1988. ISBN 0-19-510515-X.
[11] A.N. Flynn, K.D. Hall, A. Courville, P.J. Rogers, J.M. Brunstrom, Time to revisit the passive overconsumption hypothesis? Humans show sensitivity to calories in energy-rich meals, Am. J. Clin. Nutr. 116 (2022) 581–588, https://doi.org/10.1093/ajcn/nqac112.
[12] R.J. Stubbs, D.A. Hughes, E. Rowley, C. Reid, M. Elia, R. Stratton, H. Delargy, N. King, J.E. Blundell, The use of visual analogue scales to assess motivation to eat in human subjects: a review of their reliability and validity with an evaluation of new hand-held computerized systems for temporal tracking of appetite ratings, Br. J. Nutr. 84 (2000) 405–415, https://doi.org/10.1017/s0007114500001719.
[13] M.I. Friedman, P. Ulrich, R.D. Mattes, A figurative measure of subjective hunger sensations, Appetite 32 (1999) 395–404, https://doi.org/10.1006/appe.1999.0230.
[14] A. Harris, J. Wardle, The feeling of hunger, Br. J. Clin. Psychol. 26 (1987) 153–154, https://doi.org/10.1111/j.2044-8260.1987.tb00745.x.
[15] L.F. Monello, J. Mayer, Hunger and satiety sensations in men, women, boys and girls, Am. J. Clin. Nutr. 20 (1967) 253–261, https://doi.org/10.1093/ajcn/20.3.253.
[16] J.T. Cacioppo, W. von Hippel, J.M. Ernst, Mapping cognitive structures and processes through verbal content: the thought-listing technique, J. Consult. Clin. Psychol. 65 (1997) 928–940, https://doi.org/10.1037//0022-006x.65.6.928.
[17] M.I.H. Khan, T. Farrell, S.A. Nagy, M. Karim, Fundamental understanding of cellular water transport process in bio-food material during drying, Sci. Rep. 8 (2018) 15191, https://doi.org/10.1038/s41598-018-33159-7.
[18] G. Camps, R. Veit, M. Mars, C. de Graaf, P.A.M. Smeets, Just add water: effects of added gastric distension by water on gastric emptying and satiety related brain activity, Appetite 127 (2018) 195–202, https://doi.org/10.1016/j.appet.2018.04.023.
[19] G. Camps, M. Mars, C. de Graaf, P.A.M Smeets, A tale of gastric layering and sieving: gastric emptying of a liquid meal with water blended in or consumed separately, Physiol. Behav. 176 (2017) 26–30, https://doi.org/10.1016/j.physbeh.2017.03.029.
[20] L. Marciani, N. Hall, S.E. Pritchard, E.F. Cox, J.J. Totman, M. Lad, C.L. Hoad, T.J. Foster, P.A. Gowland, R.C. Spiller, Preventing gastric sieving by blending a solid/water meal enhances satiation in healthy humans, J. Nutr. 212 (2012) 1253–1258, https://doi.org/10.3945/jn.112.159830.
[21] G.H. Anderson, D. Woodend, Consumption of sugars and the regulation of short-term satiety and food intake, Am. J. Clin. Nutr. 78 (suppl) (2003) 843S–849S, https://doi.org/10.1093/ajcn/78.4.843S.
[22] P.J. Rogers, J.-.A. Carlyle, A.J. Hill, J.E. Blundell, Uncoupling sweet taste and calories: comparison of the effects of glucose and three intense sweeteners on hunger and food intake, Physiol. Behav. 43 (1988) 547–552, https://doi.org/10.1016/0031-9384(88)90207-7.
[23] P.M. Hellström, P. Grybäck, H. Jacobsson, The physiology of gastric emptying, Best Pract. Res. Clin. Anaesthesiol. 20 (2006) 397–407, https://doi.org/10.1016/j.bpa.2006.02.002.

[24] E. Almiron-Roig, L. Palla, K. Guest, C. Ricchiuti, N. Vint, S.A. Jebb, A. Drewnowski, Factors that determine energy compensation: a systematic review of preload studies, Nutr. Rev. 71 (2013) 458–473, https://doi.org/10.1111/nure.12048.
[25] P.J. Rogers, J.E. Blundell, Separating sweetness and calories: effects of saccharin and carbohydrates on hunger and food intake in human subjects, Physiol. Behav. 45 (1989) 1093–1099, https://doi.org/10.1016/0031-9384(89)90093-0.
[26] J. Wardle, Hunger and satiety: a multidimensional assessment of responses to caloric loads, Physiol. Behav. 40 (1987) 577–582, https://doi.org/10.1016/0031-9384(87)90100-4.
[27] D. Lakens, Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for *t*-tests and ANOVAs, Front. Psychol. 4 (2013) 863, https://doi.org/10.3389/fpsyg.2013.00863.
[28] D.C. Howell, Statistical Methods for Psychology, Duxbury Press, Belmont CA, 1997.
[29] Pardiwalla, S. (2012). Nice AND Naughty: Attitudes Towards Chocolate and Their Role in Determining Its Mood and Appetite Effects. PhD thesis, University of Bristol.
[30] W. Han, L.A. Tellez, M.H. Perkins, I.O. Perez, T. Qu, J. Ferreira, T.L. Ferreira, D. Quinn, Z.-.W. Lui, X.-.B. Gao, M.M. Kaelberer, D.V. Bohórquez, S.J. Shammah, G. de Lartigue, I.E. de Aarujo, A neural circuit for gut-induced reward, Cell 175 (2018) 1–14, https://doi.org/10.1016/j.cell.2018.08.049.
[31] A. Sclafani, K. Ackroff, The relationship between food reward and satiation revisited, Physiol. Behav. 82 (2004) 89–95, https://doi.org/10.1016/j.physbeh.2004.04.045.
[32] M.P. Lasschuijt, K. de Graaf, M. Mars, Effects of oro-sensory exposure on satiation and underlying neurophysiological mechanisms - what do we know so far? Nutrients 13 (2021) 1391, https://doi.org/10.3390/nu13051391.
[33] M.R. Yeomans, Flavour-nutrient learning in humans. An elusive phenomenon? Physiol. Behav. 106 (2012) 345–355, https://doi.org/10.1016/j.physbeh.2012.03.013.
[34] H.P. Weingarten, O.T. Kulikovski, Taste-to-postingestive consequence conditioning: is the rise in sham feeding with repeated experience a learning phenomenon? Physiol. Behav. 45 (1989) 471–476, https://doi.org/10.1016/0031-9384(89)90060-7.
[35] P.J. Rogers, D. Ferriday, S.A. Jebb, J.M. Brunstrom, Connecting biology with psychology to make sense of appetite control, Nutr. Bull. 41 (2016) 344–352, https://doi.org/10.1111/nbu.12237.
[36] G.J. Wang, D. Tomasi, W. Backus, R. Wang, F. Telang, A. Geliebter, J. Korner, A. Bauman, J.S. Fowler, P.K. Thanos, N.D. Volkow, Gastric distention activates satiety circuitry in the human brain, Neuroimage 39 (2008) 1824–1831, https://doi.org/10.1016/j.neuroimage.2007.11.008.
[37] A.L. Carreiro, J. Dhillon, S. Gordon, A.G. Jacobs, K.A. Higgins, B.M. McArthur, B. W. Redan, R.L. Rivera, L.R. Schmidt, R.D. Mattes, The macronutrients, appetite and energy intake, Annu. Rev. Nutr. 36 (2016) 73–103, https://doi.org/10.1146/annurev-nutr-121415-112624.
[38] E. Stephan, J.V. Pardo, P.L. Faris, B.K. Hartman, S.W. Kim, E.H. Ivanov, R. S. Daughters, P.A. Costello, R.L. Goodale, Functional neuroimaging of gastric distention, J. Gastrointest. Surg. 7 (2003) 740–749, https://doi.org/10.1016/s1091-255x(03)00071-4.
[39] A. Geliebter, Neuroimaging of gastric distension and gastric bypass surgery, Appetite 71 (2013) 459–465, https://doi.org/10.1016/j.appet.2013.07.002.
[40] S. Higgs, A.C. Williamson, P. Rotshtein, G.W. Humphreys, Sensory-specific satiety is intact in amnesics who eat multiple meals, Psychol. Sci. 19 (2008) 623–628, https://doi.org/10.1111/j.1467-9280.2008.02132.x.
[41] P. Rozin, S. Dow, M. Moscovitch, S. Rajaram, What causes humans to begin and end a meal? A role for memory for what has been eaten, as evidenced by a study of multiple meal eating in amnesic patients, Psychol. Sci. 9 (1998) 392–396, https://doi.org/10.1111/1467-9280.00073.
[42] J.E. Cecil, J. Francis, N.W. Reid, Relative contributions of intestinal, gastric, oro-sensory influences and information to changes in appetite induced by the same liquid meal, Appetite 31 (1998) 377–390, https://doi.org/10.1006/appe.1998.0177.
[43] I.M. Chapman, E.A. Goble, G.A. Wittert, J.E. Morley, M. Horowitz, Effect of intravenous glucose and euglycemic insulin infusions on short-term appetite and food intake, Am. J. Physiol.: Regul. Integr. Compar. Physiol. 274 (1998) R596–R603, https://doi.org/10.1152/ajpregu.1998.274.3.R596.
[44] K.P. Myers, M.S. Taddeo, E.K. Richards, Sensory-specific appetition: postingestive detection of glucose rapidly promotes continued consumption of a recently encountered flavor, Physiol. Behav. 121 (2013) 125–133, https://doi.org/10.1016/j.physbeh.2013.03.021.
[45] A. Sclafani, Gut-brain nutrient signaling. Appetition vs. satiation, Appetite 71 (2013) 454–458, https://doi.org/10.1016/j.appet.2012.05.024.
[46] M. Zajac, E. Modrzejewski, Z. Jankowska, The role of gastric mechanoreceptor function in the regulation of behaviour patterns induced with thirst or hunger in rats, Acta Physiol. Pol. 36 (1985) 85–91. PMID: 3837593.
[47] P.J. Rogers, F.D.Y. Drumgoole, E. Quinlan, Y. Thompson, An analysis of sensory-specific satiation: food liking, food wanting, and the effects of distraction, Learn. Motiv. 73 (2021), 101688, https://doi.org/10.1016/j.lmot.2020.101688.
[48] L. Seguias, K. Tapper, The effect of mindful eating on subsequent intake of a high calorie snack, Appetite 121 (2018) 93–100, https://doi.org/10.1016/j.appet.2017.10.041.
[49] K.N. Frayn, R.D. Evans, Human Metabolism: A Regulatory Perspective, Wiley-Blackwell, Hoboken NJ. ISBN, 2019. Fourth edition978-1-119-33143-8.
[50] V.B. Lu, F.M. Gribble, F. Reimann, Nutrient-induced cellular mechanisms of gut hormone secretion, Nutrients 13 (2021) 883, https://doi.org/10.3390/nu13030883.