

Salt Promotes Passive Overconsumption of Dietary Fat in Humans^{1–3}

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Abstract

Background: Excess fat consumption has been linked to the development of obesity. Fat and salt are a common and appetitive combination in food; however, the effect of either on food intake is unclear. Fat taste sensitivity has been negatively associated with dietary fat intake, but how fat taste sensitivity influences the intake of fat within a meal has, to our knowledge, not yet been investigated.

Objectives: Our objectives were, first, to investigate the effects of both fat and salt on ad libitum food intake and, second, to investigate the effects of fat taste sensitivity on satiation responses to fat and whether this was affected by salt.

Methods: Forty-eight healthy adults [16 men and 32 women, aged 18–54 y, body mass index (kg/m²): 17.8–34.4] were recruited and their fat taste sensitivity was measured by determination of the detection threshold of oleic acid (18:1n–6). In a randomized 2 × 2 crossover design, participants attended 4 lunchtime sessions after a standardized breakfast. Meals consisted of elbow macaroni (56%) with sauce (44%); sauces were manipulated to be 1) low-fat (0.02% fat, wt:wt)/low-salt (0.06% NaCl, wt:wt), 2) low-fat/high-salt (0.5% NaCl, wt:wt), 3) high-fat (34% fat, wt:wt)/low-salt, or 4) high-fat/high-salt. Ad libitum intake (primary outcome) and eating rate, pleasantness, and subjective ratings of hunger and fullness (secondary outcomes) were measured.

Results: Salt increased food and energy intakes by 11%, independent of fat concentration ($P = 0.022$). There was no effect of fat on food intake ($P = 0.6$), but high-fat meals increased energy intake by 60% ($P < 0.001$). A sex × fat interaction was found ($P = 0.006$), with women consuming 15% less by weight of the high-fat meals than the low-fat meals. Fat taste sensitivity was negatively associated with the intake of high-fat meals but only in the presence of low salt (fat taste × salt interaction on delta intake of high-fat – low-fat meals; $P = 0.012$).

Conclusions: The results suggest that salt promotes passive overconsumption of energy in adults and that salt may override fat-mediated satiation in individuals who are sensitive to the taste of fat. This trial was registered at the Australian New Zealand Clinical Trials Registry (www.anzctr.org.au) as ACTRN12615000048583. *J Nutr* 2016;146:838–45.

Keywords: salt, fat, ad libitum food intake, satiation, fat taste sensitivity

Introduction

Excess dietary fat consumption is recognized as a strong contributing factor in the development of overweight and obesity (1, 2). Foods high in dietary fat have a weak effect on satiation and easily lead to overconsumption of energy due to their high energy density (3–6). Fat and salt (sodium chloride) provide a common and appetitive combination in highly consumed foods such as crisps, chips, meat, cheese, and various fast foods (7).

The role of salt in the overconsumption of energy and the development of obesity deserves more attention (8, 9). A recent Korean survey showed that, when corrected for energy intake, obese persons have higher intakes of salt (10). Moreover, a liking for salty and fatty foods was associated with higher total daily energy intakes in adults (7), uncontrolled eating (11), and overweight in children (12) than was a liking for sweet and fatty foods.

When salt is added to food, palatability increases, which consequently leads to greater food intake (13–15). The role of fat on palatability and food intake is complex (9, 16, 17). Increases in fat content do not always lead to increases in pleasantness but seem to depend on combinations with either salt or sugar (18–20). We recently found that variations in salt content are more closely related to food pleasantness than variations in fat content (21). Therefore, salt may act as a vehicle that stimulates the intake of fatty foods.

Satiety responses to dietary fat vary between individuals (22–24). Oral and gastrointestinal sensitivity to FAs appears to be

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³ Supplemental Table 1 is available from the “Online Supporting Material” link in the online posting of the article and from the same link in the online table of contents at <http://jn.nutrition.org>.

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one factor influencing the satiating efficiency of dietary fat. Some studies have found that fat taste sensitivity (i.e., oral sensitivity to FAs) is related to dietary fat intake, with those who are more sensitive to fat habitually consuming less dietary fat than those who are less sensitive (25, 26). Changes in fat taste sensitivity have also been seen after manipulation of dietary fat intake over 4-wk (27) and 6-wk (28) periods. A recent study found that individuals who are more sensitive to fat taste have stronger satiety responses to fat (i.e., the capacity of a food, in this case fat, to control subsequent hunger and eating) (29). To our knowledge, it has not yet been investigated whether fat taste sensitivity influences satiation (i.e., meal size or intrameal satiety) from fat. If there is an effect of fat taste sensitivity on satiation from fat, it is not known whether this effect is influenced by increasing palatability by the addition of salt.

We hypothesized that salt plays a major role in ad libitum food intake, whereas fat has a more passive role but a greater impact on energy intake. Second, we hypothesized that individuals who are more sensitive to the taste of fat will have stronger satiation responses to fat in foods [consuming less of high-fat (HF)⁴ than of low-fat (LF) meals] than less sensitive individuals. In addition, we hypothesized that the effect of fat taste sensitivity on fat-mediated satiation is weaker in high-salt (HS) foods than in low-salt (LS) foods.

Methods

Experimental design. This study was designed as a 2 × 2 crossover study in which participants consumed 4 lunches ad libitum—1) LF/LS, 2) LF/HS, 3) HF/LS, or 4) HF/HS—on 4 separate days after a standardized breakfast. The order of the 4 lunches was randomly assigned between participants according to the Williams design. The LS meals did not contain any added salt, and the salt concentration in the HS meals was estimated to have optimal pleasant saltiness on the basis of previous studies (15, 21, 30). In addition, fat taste sensitivity was established in duplicate by determination of the threshold of oleic acid (18:1n-6), which was assessed in 2 separate sessions.

Participants. The number of participants needed was calculated to be 49 on the basis of a 10% difference in intake (in g) between LS and HS meals (15), with the following assumptions: $\alpha = 0.05$, 2-sided, power of 80%, and a variation of 25%. Fifty-six participants between 18 and 55 y of age were recruited (January–April 2015) at Deakin University, Victoria, Australia; and data collection occurred between 17 February and 21 May 2015. Exclusion criteria were as follows: smoking, gained or lost >5 kg weight during the past year, lack of appetite, difficulties with eating or swallowing, pregnancy, and breastfeeding. Three participants dropped out before the commencement of the study, and 5 participants dropped out after the first session because of work-related issues, wheat intolerance, or dislike of the food. The remaining 48 participants (16 men) were aged between 18 and 54 y (mean \pm SD: 25 \pm 6 y). The BMI (in kg/m²) range was between 17.8 and 34.4 (mean \pm SD: 23.8 \pm 3.9). The dietary restraint score of participants was measured according to factor 1 of the Three-Factor Eating Questionnaire (31). The mean \pm SD restraint score was 8.2 \pm 3.8. Participants were informed about the procedure of the study and gave written consent before participation. This study was conducted according to the guidelines laid down in the Declaration of Helsinki, and the Deakin University Human Research Ethics Committee approved all procedures involving human participants. The checklist published in the CONSORT (Consolidated Standards of Reporting Trials) statement (32) was used for preparation of this report. This study was registered at the Australian New Zealand Clinical Trials Registry (ANZCTR, ACTRN12615000048583).

Test foods. The ad libitum lunch consisted of 750 g cooked elbow macaroni (Coles home brand) with 600 g sauce. The nutrient compositions of the meals were calculated by using Foodworks7 (Xyris Software) (Table 1). The LF/LS sauce consisted of 100% (600 g) tomato passata [0.2% fat, 0.08% NaCl, wt:wt; Remano (ALDI)]. The LF/HS sauce consisted of 100% (600 g) tomato passata with 3.3 g NaCl (0.2% fat, 0.5% NaCl, wt:wt). The HF/LS sauce consisted of 60% (360 g) tomato passata, 30% (180 g) canola oil (Coles home brand), and 10% (60 g) thickened cream sauce (34% fat, 0.06% NaCl, wt:wt; Coles home brand). The HF/HS sauce had the same ingredients as the HF/LS sauce with the addition of 3.3 g NaCl (34% fat, 0.5% NaCl, wt:wt). The HF sauces were homogenized for 3 min at 10,000 rpm (Silverson L4RT homogenizer). A concentration of 0.5% NaCl in the sauce was expected to be an optimal pleasant salt concentration (15, 21, 30).

Plain mini-croissants (Coles home brand) were used as a standardized breakfast. The macronutrient composition was as follows: 8.5 g protein, 46.8 g carbohydrate, 26 g fat, 382 mg sodium, and 1800 kJ (429 kcal) energy/100 g. The number of served croissants was calculated for each subject separately on the basis of 18% of energy of daily energy needs. The daily energy needs for each subject were estimated by the Schofield I equation (33), taking into account sex, age, and weight.

Procedures. Participants attended 6 sessions over 6 d at the Centre of Advanced Sensory Science at Deakin University. In 4 sessions, separated by ~1 wk, participants consumed a standardized breakfast at either 0830 or 0930 h and an ad libitum lunch at either 1230 or 1330 h, respectively. Fat taste sensitivity was assessed in the other 2 sessions, as described below. Participants' height (cm) and weight (kg) were measured at the first visit.

Participants were required to consume all of the served breakfast (croissants) and were allowed to drink water. Participants were instructed not to eat or drink (except for water) between breakfast and lunch. In the ad libitum lunch sessions, participants completed a questionnaire to determine whether they ate or drank anything between the meals.

At the ad libitum lunch sessions, participants were served macaroni with sauce and were instructed to eat until comfortably full. The total amount served was 1350 g, so that participants could eat as much as they wanted without asking for more; this excessive amount was expected to diminish the effects of self-monitoring the amount consumed (34). In addition, participants received a jug of water and were allowed to drink as much water as they wanted.

Ad libitum intake, eating rate, and appetite and hedonic ratings. The ad libitum food intake was calculated as the difference in the weight of the bowl with food before and after intake. The intake in grams was used to calculate the energy intake expressed in kilojoules. The eating rate (g or kJ/min) was calculated by dividing the ad libitum food or energy intake by the total eating duration (min). Participants were instructed to turn on a light as soon as they started eating, and as soon as they had finished the researcher assessed the eating duration (s) by using a stopwatch. In addition, the amount of water that participants drank was reported by weighing the jug with water before and after the lunch.

TABLE 1 Nutrient composition of 4 meals containing different combinations of 2 amounts of salt and fat¹

| | LF/LS | LF/HS | HF/LS | HF/HS |
|---------------------|-------|-------|-------|-------|
| Energy, kJ | 412 | 412 | 945 | 945 |
| Protein, g | 3.6 | 3.6 | 3.5 | 3.5 |
| Fat, g | 0.6 | 0.6 | 15.5 | 15.5 |
| Carbohydrate, g | 18.3 | 18.3 | 17.6 | 17.6 |
| Sodium, mg | 15 | 95 | 11 | 92 |
| Sodium chloride, mg | 38 | 241 | 28 | 234 |

¹ The nutrient composition of the meals (44% sauce and 56% elbow macaroni) per 100 g was calculated by using Foodworks7 (Xyris Software). HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

⁴ Abbreviations used: CCK, cholecystokinin; HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt; PYY, peptide YY.

Participants completed several appetite and hedonic questions before and upon completion of the lunch by using Compusense Five Software version 5.2 (Compusense, Inc.). They rated their feelings of hunger, fullness, prospective consumption, and thirst. When the food was served, subjects tasted 1 bite of their meal and rated the perceived pleasantness of and their desire to eat the served meals. All of the questions were answered by using a 100-mm visual analog scale that was scaled from “not at all” (0) to “very much” (100).

Fat taste sensitivity. The threshold for oleic acid was assessed by an ascending method of the 3-alternative forced-choice test, in duplicate, in 2 different sessions (35). For test sample preparation, oleic acid was mixed at varying concentrations (0.02, 0.06, 1, 1.4, 2, 2.8, 3.8, 5, 6.4, 8, 9.8, 12, and 20 mM) with long-life skim milk (99.9% fat-free; Devondale). Textural cues were minimized with an addition of 5% (wt:vol) gum acacia (Deltagen) and 5% liquid paraffin (vol:vol; Merck). To prevent oxidation, samples were mixed with 0.01% (wt:vol) EDTA (Merck). Samples were homogenized for 30 s/100 mL solution (Silverson L4RT homogenizer). Control samples were prepared in the same manner but without the addition of oleic acid.

Participants were instructed to refrain from drinking (except for water) and eating at least 1 h before the start of each session. To prevent confounding from nonoral sensory inputs, participants wore nose clips and milk samples were presented under red-light conditions. Participants were presented with 3 milk samples [1 sample that contained the FA (starting with the lowest concentration) and 2 controls] and were asked to select the sample that tasted different from the other 2. After an incorrect response, a higher FA concentration was presented. After a correct response, the same FA concentration was presented. The detection threshold was defined as the concentration that was identified correctly 3 consecutive times. Eight participants showed a detection threshold that differed by >3 concentrations when measured in 2 different sessions. These participants were invited for a third session, after which the 2 closest measured detection thresholds were averaged and the outlying measurement was omitted (35).

Statistical analyses. Statistical analyses were performed by using SAS version 9.3 (SAS Institute). Data are presented as means or adjusted means \pm SEMs. *P* values <0.05 were considered to be significant. Effects of fat (LF compared with HF) and salt (LS compared with HS) and their interaction on ad libitum food and energy intakes, eating rate, pleasantness, and desire to eat were tested in a mixed linear model (PROC MIXED) that included the participant as the repeated factor. Sex had an effect on intake, pleasantness, and desire to eat, although only for fat and not for salt (see Results); therefore, sex \times fat was included as a covariate in the mixed linear model. The order of presentation had an effect on intake only for fat; therefore, order \times fat was also included as a covariate in the mixed linear model on intake. Dietary restraint score, age, and BMI did not affect ad libitum intake and were therefore not included in the mixed model.

Appetite ratings from before compared with after lunch within a session were assessed with paired *t* tests. The effects of fat and salt and their interaction on delta appetite ratings (after intake – before intake) were tested in a similar mixed linear model as described above.

The effects of fat taste sensitivity (detection threshold of oleic acid), salt, and salt \times fat taste sensitivity on delta food intake of HF compared with LF meals were assessed in a generalized linear model that included order and sex. The delta food intakes of HF compared with LF meals between the most sensitive participants [expressed in different percentages (25–75%) for who had the lowest detection threshold of oleic acid] compared with the remaining participants were assessed in generalized linear models (separately for LS and HS) that included order and sex. Tukey-Kramer adjustments were used for all post hoc comparisons. Pearson correlation coefficients were calculated to assess relations between various outcome measurements.

Results

Effects of fat and salt on ad libitum food and energy intakes.

840 Bolhuis et al.

(*P* = 0.022) and energy intake (*P* = 0.031) compared with the LS meals (Figure 1). Fat did not affect food intake (*P* = 0.60), but the HF meals resulted in an ~60% higher energy intake compared with the LF meals (*P* < 0.001) (Figure 1B). No salt \times fat interactions were observed for food (*P*-interaction = 0.95) or energy (*P*-interaction = 0.61) intakes. There were sex \times fat effects for food (*P*-interaction = 0.006) and energy (*P*-interaction < 0.001) intakes, with the differences between men and women reported below. In addition, there were order \times fat effects on food (*P*-interaction = 0.023) and energy (*P*-interaction = 0.003) intakes; participants consumed less food and energy with the HS meals when presented for the second time than when served the first time. Salt did not interact with sex or meal order to affect ad libitum food or energy intake.

Participants drank 166 \pm 20 g water with the LF/LS meal, 226 \pm 25 g water with the LF/HS meal, 182 \pm 20 g water with the HF/LS meal, and 262 \pm 41 g water with the HF/HS meal. Water consumption was affected by salt (*P* = 0.002) but not by fat (*P* = 0.15). Water intake (in g) and food intake did not correlate in any of the 4 meals (LF/LS: *r* = 0.15; LF/HS: *r* = 0.10; HF/LS: *r* = 0.03; HF/HS: *r* = -0.08; all *P* > 0.3).

Pleasantness, eating rate, and BMI. There was a main effect for salt (*P* < 0.001) but not for fat (*P* = 0.90) on pleasantness (Figure 2). Ratings of desire to eat the meals also showed a higher desire for the HS meals than for the LS meals (*P* = 0.033), but no effect of fat was observed (*P* = 0.83). The eating rate expressed as g/min was not affected by fat or salt content (Table 2); however, eating rate was affected by fat when expressed as kJ/min.

Food intake was positively correlated with eating rate (g/min; LF/LS: *r* = 0.56; HF/LS: *r* = 0.52; HF/HS: *r* = 0.69; all *P* < 0.001); however, this was not significant for the LF/HS meal (*P* = 0.18). Food intake was positively correlated with pleasantness ratings, although this was significant only for the HF meals [*r* = 0.50

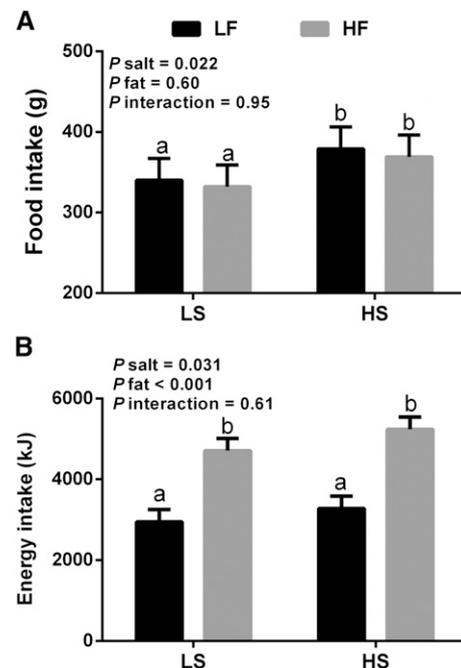


FIGURE 1 Ad libitum food (A) and energy (B) intakes of healthy adults who consumed 4 meals containing different combinations of 2 amounts of salt and fat in random order. Values are adjusted means \pm SEMs, corrected for sex and order effects; *n* = 48. Labeled means without a common letter differ, *P* < 0.05. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

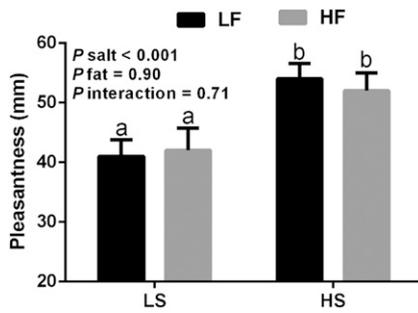


FIGURE 2 Pleasantness ratings by healthy adults who consumed 4 meals containing different combinations of 2 amounts of salt and fat as measured on a visual analog scale. Values are adjusted means \pm SEMs, corrected for sex and order effects; $n = 48$. Labeled means without a common letter differ, $P < 0.05$. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

($P < 0.001$) and $r = 0.32$ ($P = 0.028$) for the LS and HS meals, respectively]. Eating rate (g/min) was positively correlated with pleasantness; however, this was significant only for the HF meals [$r = 0.35$ ($P = 0.016$) and $r = 0.34$ ($P = 0.019$) for the LS and HS meals, respectively]. BMI was positively correlated with food intake for the HF/HS meal ($r = 0.34$, $P = 0.019$) but was not significant for the other meals. BMI was not significantly correlated with delta food intake of HF compared with LF meals (i.e., difference in food intake of HF and LF meals) for both LS and HS meals (both $P > 0.19$) but was positively correlated with eating rate (g/min) for each meal ($r = 0.29$ – 0.37 ; all $P < 0.05$).

Sex differences. Sex effects were found for fat on food intake, pleasantness, and desire to eat. Significant interactions of sex \times fat were found for food and energy intakes as described above. Women had 15% less intake by weight of the HF meals compared with the LF meals ($P = 0.036$), but men did not ($P = 0.55$) (Figure 3). Moreover, both pleasantness and desire to eat showed sex \times fat interactions (P -interaction = 0.016 and 0.006, respectively). Post hoc comparisons showed higher desire to eat for the HF meals than for the LF meals for men ($P = 0.046$) but not for women ($P = 0.17$). Eating rate (g/min) was not affected by sex ($P = 0.50$) or sex \times fat ($P = 0.12$). There were no sex \times salt interactions on food or energy intakes, pleasantness, or desire to eat (all $P > 0.18$). Dietary restraint scores did not differ between men and women (7.9 ± 1.1 compared with 8.4 ± 0.6 , respectively; $P = 0.65$).

Appetite ratings. Ratings of hunger, fullness, and prospective consumption before lunch did not differ between meals (Table 3), indicating that participants were in a similar state of satiety before ad libitum intake. Hunger ratings decreased, fullness increased, and ratings of prospective consumption decreased

significantly after ad libitum intake of each meal (all $P < 0.001$). Thirst decreased after the LF/LS, HF/LS, and HF/HS meals ($P < 0.05$) but not after the LF/HS condition ($P = 0.20$). There were no main effects of fat on decrease in hunger (delta), increase in fullness, or decrease in ratings of prospective consumption (Table 3). HS meals resulted in a stronger decrease in prospective consumption and tended to result in a stronger decrease in hunger ($P = 0.20$) compared with the LS meals (Table 3).

Fat taste sensitivity and food intake of HF compared with LF meals. The intraclass correlation for the 2 measured detection thresholds of oleic acid between participants was 0.84 (95% CI: 0.70, 0.90; $P < 0.001$). The frequency distribution of the mean detection thresholds is shown in Supplemental Table 1. The mean detection threshold for all participants was 4.6 ± 0.35 mM. Fat taste sensitivity did not significantly differ between men and women (men: 4.5 ± 1.1 mM; women: 4.7 ± 0.9 mM; $P = 0.92$). There was no correlation between fat taste sensitivity and BMI ($r = 0.03$, $P = 0.83$). To assess the effects of fat taste sensitivity on differences in food intake of HF compared with LF meals, the delta food intake (intake of HF meal – intake of LF meal) was calculated for both LS and HS meals. There was no main effect of fat taste sensitivity on delta food intake ($P = 0.18$) and no main effect of salt ($P = 0.92$); however, there was a significant fat taste sensitivity \times salt interaction (P -interaction = 0.012).

Figure 4 shows the delta food intakes of the most sensitive participants against the remaining less sensitive participants. The most sensitive 25% [$n = 12$ (3 males), threshold oleic acid ≤ 1.4 mM, Figure 4A] and 33% [$n = 15$ (4 males) threshold oleic acid ≤ 1.7 mM, Figure 4B] consumed less of the HF meals compared with the LF meals than the least sensitive participants consumed, but only for LS meals. Despite differences in food intake, changes in appetite ratings (i.e., decrease in hunger and prospective consumption and increase in fullness) after consumption of the HF/LS meals did not differ significantly between the 25% or 33% most sensitive participants compared with the remaining participants (all $P > 0.30$). Figure 5 shows the delta food intake (HF meals – LF meals) plotted against percentages of the most sensitive participants for both LS and HS meals separately. The difference between HF and LF meals disappeared when the sensitivity decreased (increasing percentage of the most sensitive participants) in the LS meals, whereas this effect was not observed in the HS meals.

Discussion

The results show that salt increased food and energy intakes by 11% independent of fat concentration. The addition of salt, but not fat, increased pleasantness, which probably explains the higher food intake due to salt. The higher intake of the HS meals

TABLE 2 Eating rates and meal durations by healthy adults who consumed 4 meals containing different combinations of 2 amounts of salt and fat in random order¹

| | LF/LS | LF/HS | HF/LS | HF/HS | P | | |
|----------------------------|---------------------------|---------------------------|---------------------------|---------------------------|--------|------|-------------------|
| | | | | | Fat | Salt | Fat \times salt |
| Eating rate, g/min | 55 \pm 4.2 | 59 \pm 4.4 | 52 \pm 4.4 | 56 \pm 4.9 | 0.94 | 0.26 | 0.97 |
| Energy intake rate, kJ/min | 475 \pm 37 ^a | 507 ^a \pm 38 | 741 \pm 62 ^b | 799 \pm 70 ^b | <0.001 | 0.31 | 0.73 |
| Meal duration, min | 6.8 \pm 0.5 | 7.4 \pm 0.6 | 6.4 \pm 0.6 | 6.5 \pm 0.4 | 0.14 | 0.24 | 0.53 |

¹ Values are adjusted means \pm SEMs, corrected for sex and order effects; $n = 48$. Labeled means in a row without a common superscript letter differ, $P < 0.05$. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

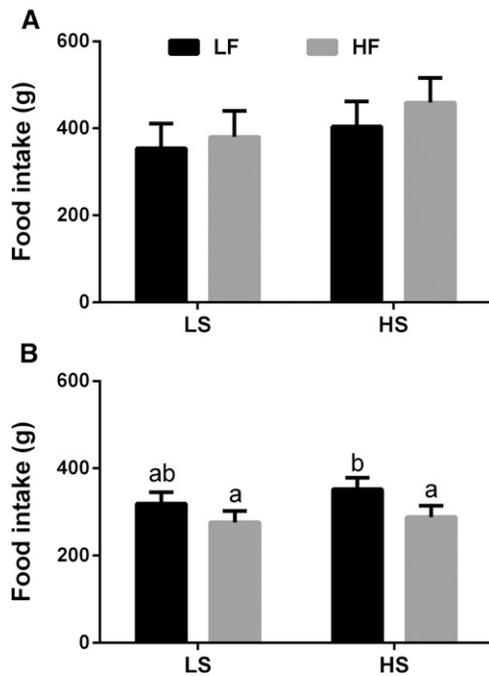


FIGURE 3 Ad libitum food intakes of men (A) and women (B) who consumed 4 meals containing different combinations of 2 amounts of salt and fat in random order. Values are adjusted means + SEMs, corrected for order effects; $n = 16$ men and 32 women. Labeled means without a common letter differ, $P < 0.05$. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

was accompanied by stronger decreases in ratings of prospective consumption and hunger, whereas this was not influenced by fat. The excessive increase in fat content (0.6 compared with 15.5 g/100 g and 6% compared with 62% of energy from fat) hardly affected intake in grams but led to a 60% higher energy intake. The present study emphasizes how dietary fat easily leads to overconsumption of energy within a meal. However, the participants with the lowest fat taste thresholds (most sensitive to fat) consumed less of the HF meals than of the LF meals, but only in the LS condition. In addition to the overall effect of salt in driving

passive overconsumption of fat, these results suggest that salt overrides fat-mediated satiation in fat taste-sensitive individuals.

We did not find interaction effects of salt and fat on food intake, which indicates independent effects. The present study shows that fat does not necessarily need salt for the consumption of excess energy. However, in real-life situations, foods high in dietary fat are most likely accompanied by a salty, savory, or sweet taste and are not just a fatty tasting food (7, 36–38). In this perspective, salt does promote overconsumption of dietary fat, simply because fatty foods without another dominant taste are not common and are unlikely to be consumed. In line with this, others have proposed that sugar may act as a vehicle that drives fat intake (38). Meals containing mostly salty/savory foods and high-fat foods at meals were found to have greater potential to influence daily energy intake than were snacks (5), probably because meals are larger eating episodes and therefore give greater opportunity to overconsume. This suggests an important role for salt in the overconsumption of dietary fat.

As expected, the HS meals led to greater water consumption than the LS meals. Participants were free to consume as much water as they wanted. The results showed no relation between food and water intakes, which is in line with a study that clearly showed that drinking water with meals does not interfere with food intake (39).

In the present study, the 33% of participants who were most sensitive to fat taste consumed less of the HF meal than of the LF meal. This is in line with previous studies showing that fat taste sensitivity is negatively related to intake of dietary fat (25–28). The present study showed stronger satiation responses to fat in fat taste-sensitive individuals, in addition to stronger satiety responses, which has previously been shown (29). Sensitive individuals consumed less during lunch after a fixed high-fat breakfast than after a high-protein and high-carbohydrate breakfast, whereas less sensitive individuals did not show this effect (29). Fat taste sensitivity may be related to satiety responses from FAs in the gastrointestinal tract, because both oral and gastrointestinal responses to FAs were weaker in obese compared with lean individuals (24). Together, this suggests that the lower intake of dietary fat in fat taste-sensitive individuals is possibly regulated by fat-mediated satiation, as suggested in the present study, in addition to fat-mediated

TABLE 3 Appetite ratings by healthy adults who consumed 4 meals containing different combinations of 2 amounts of salt and fat in random order¹

| | LF/LS, mm | LF/HS, mm | HF/LS, mm | HF/HS, mm | P^2 | P^3 | | |
|-------------------------|-----------|-----------|-----------|-----------|-------|-------|-------|------------|
| | | | | | | Fat | Salt | Fat × salt |
| Hunger | | | | | | | | |
| Before | 66 ± 3.0 | 66 ± 2.7 | 62 ± 3.4 | 62 ± 3.5 | 0.40 | | | |
| Δ | −45 ± 4.1 | −50 ± 3.1 | −40 ± 4.3 | −46 ± 3.8 | | 0.47 | 0.07 | 0.99 |
| Fullness | | | | | | | | |
| Before | 21 ± 2.7 | 22 ± 2.5 | 23 ± 3.2 | 25 ± 3.1 | 0.73 | | | |
| Δ | 50 ± 3.9 | 54 ± 4.0 | 47 ± 5.0 | 51 ± 3.9 | | 0.94 | 0.28 | 1.0 |
| Prospective consumption | | | | | | | | |
| Before | 64 ± 2.7 | 62 ± 2.6 | 60 ± 3.1 | 62 ± 2.8 | 0.55 | | | |
| Δ | −41 ± 3.7 | −45 ± 3.0 | −38 ± 3.5 | −44 ± 3.6 | | 0.95 | 0.046 | 0.67 |
| Thirst | | | | | | | | |
| Before | 54 ± 3.2 | 51 ± 3.7 | 56 ± 3.6 | 55 ± 3.6 | 0.60 | | | |
| Δ | −12 ± 4.0 | −7 ± 5.3 | −17 ± 3.8 | −10 ± 4.4 | | 0.30 | 0.10 | 0.84 |

¹ Values are means ± SEMs, $n = 48$. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt; Δ, rating after intake – rating before intake.

² P values representing differences between lunch sessions before intake.

³ P values representing main effects of fat and salt and their interaction.

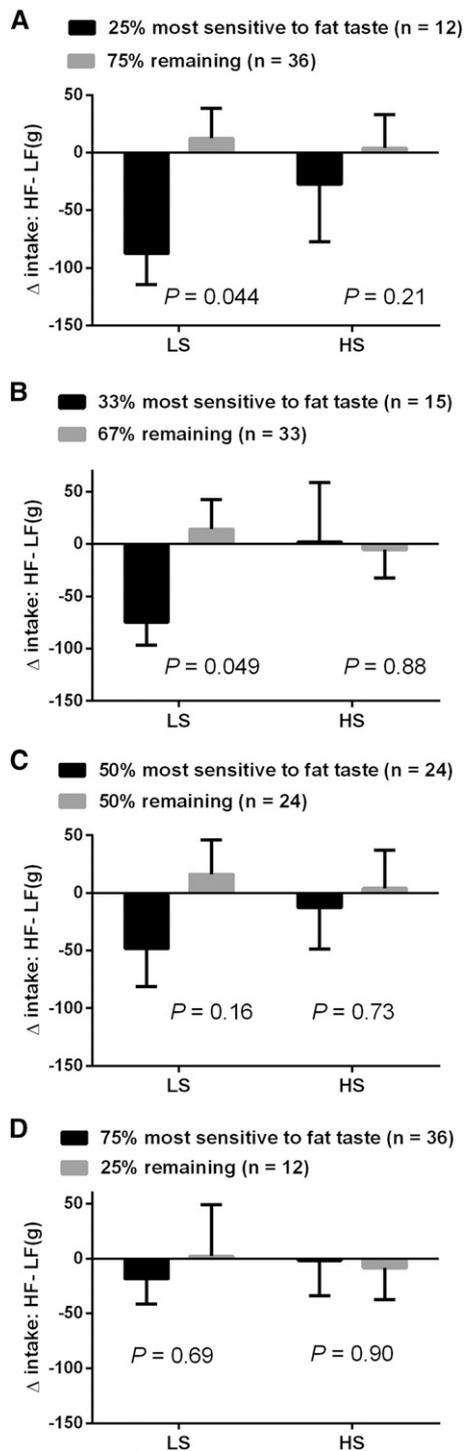


FIGURE 4 Differences in food intake for LS and HS meals according to amount of fat (Δ food intake: HF meals – LF meals) for the most sensitive (i.e., lowest detection threshold of oleic acid) 25% (A), 33% (B), 50% (C), and 75% (D) of participants compared with the remaining participants. Values are adjusted means + SEMs, corrected for sex and order effects; $n = 48$. P values in the panels are shown for the difference between the most sensitive participants compared with the remaining participants for LS and HS meals separately. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

satiety (29) and possibly also to a lower attraction to fatty foods in general.

However, we found that salt overrides the fat-mediated satiation in fat taste-sensitive individuals. This overruling effect

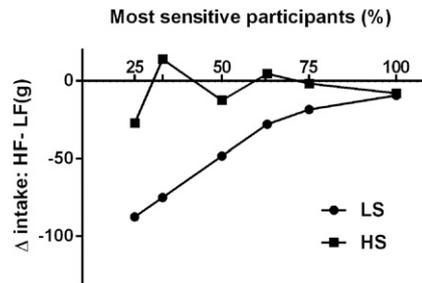


FIGURE 5 Differences in food intake according to amount of fat (Δ food intake: HF meals – LF meals) plotted against percentages of the most sensitive participants (i.e., lowest detection threshold of oleic acid) for LS and HS meals separately. Values are adjusted means, corrected for sex and order effects; $n = 48$. HF, high-fat; HS, high-salt; LF, low-fat; LS, low-salt.

of salt on fat taste perception was recently shown, whereby fat taste sensitivity was inversely related to the most preferred fat content (i.e., sensitive individuals preferred lower fat contents than did less sensitive individuals); however, this relation was nullified when salt was added (21). As discussed earlier, fatty foods in real-life situations do not just taste “fatty” but generally have another dominant taste such as salty, savory, or sweet. This means, in practice, that fat-mediated satiation in fat taste-sensitive individuals may play a minor role in adjusting for fat intake. Therefore, foods high in dietary fat are also a risk factor for overconsumption of energy for individuals with sensitive fat taste due to the other tastes or flavors present.

The role of dietary fat on the overconsumption of energy has been suggested to mainly act via satiation rather than satiety (40); however, it has been suggested that, joule-per-joule, fat also has a weak satiety efficiency compared with carbohydrates (41). The present study clearly shows that intake within a meal is not controlled by energy density, in accordance with many other studies (e.g., 39, 42–45). Given the fact that fat is the most energy-dense macronutrient compared with proteins and carbohydrates, it is easily overconsumed within a meal or snack, in line with studies showing that excessive fat intake from a single meal or snack leads to marked short-term positive energy balances (4, 5, 40, 46–48).

The relation between BMI and fat taste sensitivity remains contentious. The present study and others did not find this relation (29, 49, 50), whereas other studies did (25, 26, 51, 52). The overconsumption of energy from dietary fat acts mainly via satiation or acute food intake (40). We showed that fat-mediated satiation in fat taste-sensitive individuals is easily overruled by salt and probably also by other taste qualities or flavors in real-life situations. Therefore, the weak action of fat on satiation and the overruling factors of other flavors could be a possible explanation why relations between BMI and fat taste sensitivity are not always found.

The present study showed that women consumed less of the HF compared with the LF meals by weight, but men did not. In addition, only men but not women preferred HF meals over the LF meals. Higher liking for and intakes of fat (7) or salty and fatty foods (11) in men have been shown before. In 1 study (7), the authors explained this by a stronger dietary restraint behavior generally found in women (53). However, we did not find differences between men and women on restraint scores or an effect of restraint \times fat on food intake. The differences in visual appearance of the LF and HF meals were obvious, and awareness of fat plays a role in food intake (54), which possibly

affected women more than men. Sex effects in response to fat intake may also be explained by hormonal differences in satiety responses. Fat intake stimulates the satiety peptides cholecystokinin (CCK) and peptide YY (PYY). Estradiol was found to affect the meal intake and increased the vagal sensitivity to CCK (55). Reports on sex differences of postprandial and fasting PYY concentrations showed conflicting results and did not focus on acute meal responses (56). However, it should be noted that the sex effects of the present study need to be interpreted with care due to the low number of men compared with women.

A limitation of the study is that we measured the intake of only 1 food. We did not find a main effect of fat on pleasantness; however, this depends on the type of food. Generally, higher amounts of fat seem to be better liked in solid than in liquid foods (19, 20). Moreover, the excess fat in the HF meals was unrealistic but stresses the lack of satiation signals from the excess amount of fat in most individuals. Another limitation is that we did not measure energy compensation after the meal, but this excess energy intake was unlikely to be compensated for, at least not within a day. Others have shown that HF, energy-dense meals led to a markedly higher daily intake of energy (3, 5, 57). This is in accordance with other studies that showed poor compensation after energy overconsumption in general (58, 59).

In conclusion, an excessive increase in dietary fat (from 0.6 to 15.5 g/100g) did not have a main effect on food intake by weight; however, it led to a 60% higher energy intake. The addition of salt increased pleasantness and food and energy intakes independent of fat concentration. Therefore, salt promotes passive overconsumption of dietary fat. Individuals with sensitive fat taste are able to adjust for fat intake, although this effect seems to be overruled by the increase in pleasantness due to the addition of salt.

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DPB and RSJK designed the research; DPB and AC conducted the research; DPB analyzed data and wrote the main part of the manuscript; AC, LPN, and RSJK provided expert input and were involved in drafting of the manuscript; and RSJK had primary responsibility for final content. All authors read and approved the final manuscript.

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