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## Perception, passive overfeeding and energy metabolism

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#### Abstract

The palatability of a diet is an important determinant of energy intake. Due to a high palatability, a relatively high energy density, and a weak effect on satiation, the consumption of high-fat foods induces passive overfeeding. It is well known that a high-fat diet often leads to a loss of portion control of tasty foods. Here, studies are reviewed on the effect of overfeeding on substrate utilization and energy expenditure. It is often suggested that humans differ in the susceptibility to weight gain in response to overfeeding. Six years ago, non-exercise activity thermogenesis was presented as a new mechanism to explain differences in weight gain between subjects. Activation of non-exercise activity thermogenesis could dissipate excess energy to preserve leanness and only failure to activate non-exercise activity thermogenesis resulted in ready fat gain. However, there is still little evidence for this form of adaptive thermogenesis from additional studies. The conclusion is that the fat content has an effect on body fat as a function of the effect of dietary fat on energy intake.

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### 1. Introduction

Dietary fat is among the most important factors for the development of obesity [1]. The energy intake from fat has a greater effect on body weight than energy from non-fat sources. Eating high-fat foods facilitates the development of a positive energy balance by a lower satiating power than the other macronutrients [2]. The overconsumption on foods high in dietary fat is explained by the potent sensory qualities and high palatability of high-fat foods. Additionally, the energy value of fat, with 37kJ/g, is more than twice as high as the energy value (17kJ/g) for carbohydrate and protein [3].

Fat, as a substrate for energy metabolism, is at the bottom of the oxidative hierarchy that determines fuel selection [4]. Changes in alcohol, carbohydrate and protein intake elicit auto regulatory adjustments in oxidation whereas a change in fat intake fails to elicit such a response. There are two types of studies showing the effect of fat intake on fat oxidation, studies where fat is supplemented in excess of energy requirements and studies on the effect of high- and low-fat diets given in energy balance. Several studies have shown that fat intake does not stimulate its own oxidation when fat is consumed in excess of energy requirements [5-7]. Schrauwen et al. [8] showed that it took a week before fat oxidation was raised sufficiently to match fat intake, when diet composition was iso-energetically switched from low-fat to high-fat.

Studies on the effect of fat intake on fat oxidation and energy balance are typically performed in the confined environment of a respiration chamber, where activity energy expenditure is about 50% of the value in daily life [9]. Physical activity might be an important factor in the development of diet-induced obesity. Levine et al. [10] showed considerable interindividual variation in the susceptibility to weight gain in response to overeating and explained two-thirds from increases in nonexercise activity thermogenesis (NEAT). Here, evidence is presented from additional studies on the effect of fat intake and overfeeding on energy balance.

#### 2. Methods

Two types of studies on perception, overeating and energy metabolism will be reviewed. Firstly, studies where the percentage of fat in the diet was increased without interfering with the quantity the subjects eat, and effects are reported on energy

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balance. Secondly, studies where subjects are overfed and effects are reported on energy balance and measured energy expenditure.

There are many intervention studies where the percentage of dietary fat is changed under ad libitum food conditions. Most of the studies involve a reduction of fat intake with a fat-reduced diet. Then, the general finding is that a reduction of dietary fat causes weight loss [11]. Here, the focus will be on studies where dietary fat is increased by including high-fat foods in a diet that can be consumed ad libitum.

To study effects of overeating on individual variation in weight gain, studies were selected where subjects were overfed and effects were reported on measured energy expenditure. Here, basically two types of experimental design are available. Studies where subjects were studied under well-controlled conditions in a respiration chamber and studies where subjects were observed under normal daily living conditions and energy expenditure was measured with doubly labelled water. Respiration chamber studies typically covered interventions with a duration of some days up to a maximum of 12 days. Studies with doubly labelled water had a minimum duration of 10 to 14 days.

To study effects of dietary interventions on body mass and body composition, the size of the induced change in energy balance determines the length of the intervention for a detectable effect. For body composition, there is an uncertainty in the order of magnitude of minimally 1.5 kg fat mass and fatfree mass. A combination of independent measurements can reduce this measurement bias. In a three-compartment model, based on the measurement of body mass, body volume and total body water, the claimed precision is 1.0 kg for fat mass and 0.7 kg for fat-free mass [12]. The precision will never reach the level of 0.001 kg for body mass with integrating electronic balances. For comparative studies subjects should be measured with minimal clothing, minimal gut contents (post-absorptive) and with an empty bladder.

#### 3. Results

Lissner et al. [13] performed one of the first intervention studies on the role of dietary fat in the regulation of energy intake. They measured ad libitum food consumption on three diets that were similar in appearance but differed in the amount of high-fat ingredients used. Twenty-four women each consumed a sequence of three dietary treatments in which 15-20%, 30-35%, or 45-50% of the energy was derived from fat. Relative to their energy consumption on the medium-fat diet, the subjects spontaneously consumed an 11% deficit on the low fat diet and a 15% surfeit on the high-fat diet, resulting in significant weight changes of, respectively, -0.40 and +0.32 kg. Excess energy consumption on the high-fat diet was greater in the obese than the non-obese participants. We performed a study where 240 subjects were randomly assigned to either a group consuming reduced-fat products or a group consuming full-fat products for six months. Subjects visited at least once a week the laboratory to freely take food products, arranged in a shop setting. Measurements included energy intake, energy expenditure and body composition. Energy intake was measured with a 3-day food record at four times, evenly spread over the observation interval. At the start of the intervention, both groups consumed on average 35 en% of daily energy intake from fat. The diet intervention caused on average a change in fat intake and body fat mass in subjects of the reduced fat group of  $-5\pm$ 29 g/d to 33 en% (P<0.05) and  $+0.3\pm2.1$  kg (ns), respectively, and of  $+23\pm31$  g/d to 41 en% (P<0.0001) and  $+1.0\pm2.3$  kg (P<0.0001) in subjects of the full-fat group. The change in fat content of the diet was positively related to a change in energy intake, the latter explaining 5% of the variation in the change in body fat mass. The change in fat content of the diet had no effect on physical activity and energy expenditure. However, subjects with a higher activity level consumed more carbohydrate [14]. Subjects changing the fat content of the diet showed a consequent change in body fat mass only when energy intake changed as well [15].

Dauncey [16] measured the effect of overfeeding a diet high in fat for 24h in a respiration chamber. The level of overfeeding was 74% and there was a 10% increase in 24h energy expenditure (Table 1). Dallosso and James [17] overfed subjects one week with extra fat to increase energy intake by 50%. Subjects had two 36h sessions in a respiration chamber on a weight maintenance diet before and at the end of the overfeeding period. Energy expenditure on fat over-feeding increased by 6%. Faecal energy outputs on the maintenance and over-feeding diets were 5% and 4% of the respective gross energy intakes. Zed and James [18] measured the thermogenic response of an extra 4.3 MJ/d fat given to subjects for 6 days after a preliminary weight-maintenance diet. Fat overfeeding induced an increase in energy output amounting to 10% of the supplement's energy. Horton et al. [19] fed subjects at 150% of maintenance intake over two separate 14-day periods. Over one period, excess energy was entirely provided as fat and the other period entirely as carbohydrate. A respiration chamber was used to measure energy expenditure and nutrient oxidation before and on three days during each overfeeding period. Fat overfeeding had minimal effects on fat oxidation and total energy expenditure, leading to storage of 90-95% of excess energy. Carbohydrate overfeeding resulted in 75-85% of excess

Table 1 Changes in energy expenditure during overfeeding

Reference	overfeeding interval (d)	overfeeding (%)	expenditure change (%)	expenditure change (% of overfeeding)
[16]	1	$74{\pm}21^{a}$	$10\pm6$	$14 \pm 7$
[17]	7	$65\pm14^{b}$	6±3	$10 \pm 3$
[18]	6	50 <sup>b</sup>	5	10
[19]	14	50 <sup>b</sup>	3	6
		$50^{\circ}$	7	14
[20]	12	33 <sup>a</sup>	6	18
[19]	21	31 <sup>a</sup>	6	19
[20]	42	$49\pm6^{a}$	$13 \pm 15$	$26 \pm 30$
[10]	56	35 <sup>a</sup>	20	57
[21]	14	45 <sup>a</sup>	4	9

Overfeeding is expressed as {(Intake overfeeding-Expenditure weight maintenance)/Expenditure weight maintenance} \*100 (%). The change in energy expenditure is expressed as {(Expenditure overfeeding-Expenditure weight maintenance)/Expenditure weight maintenance} \*100 (%).

<sup>a</sup>Overfeeding a mixed diet; <sup>b</sup>overfeeding as fat; <sup>c</sup>overfeeding as carbohydrate.

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