The satiating effects of macronutrients - implications for weight control

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Summary

Obesity and overweight are now the most common pathological conditions in industrialised societies. Clearly, public health campaigns and the multi-billion dollar diet industry have largely failed in preventing insidious weight gain. Thus, the ways in which foods increase or satisfy our desire to eat is now an issue of great practical significance. The practice of counting kilojoules gives the impression that all kilojoules are oxidised with equal priority and suppress hunger to the same extent, whatever their source. This is misleading since different macronutrients are not equally directed towards oxidation or storage in the body and suppress the return of hunger to different extents. Furthermore, a food's palatability and energy density influence how much is eaten before appetite is sated. Thus, isoenergetic portions of different foods do not have the same effect on stimulating appetite and energy intake or maintaining satiety in the postprandial period. In recent times, a plethora of 'lite' products have become readily available and are assumed to assist weight control efforts because of their reduced energy content. However, some of these products may have a limited capacity to reduce total energy intakes because of their high palatability and energy density. Furthermore, psychological and metabolic responses to certain 'lite' foods may stimulate compensatory increases in later food intake. Further research is required to establish the ways in which different foods and dietary habits affect food intake and energy balance in order to develop effective dietary strategies for the prevention and treatment of overweight.

Introduction

During the last 100 years in industrialised societies, the ratio of weight to height has progressively increased in both adults and children accompanied by reductions in physical activity and carbohydrate (starch) intakes and an increased proportion of energy from fat (1, 2). The incidence of overweight has also increased rapidly in recent times and continues to rise suggesting that environmental and behavioural factors are responsible since the genetic make-up of the general population has not changed (3). The situation is serious as a quarter of the adult population in the USA, UK and Australia are currently estimated to be overweight (4-6).

Few people succeed in losing excess weight and maintaining weight reduction or avoid insidious weight gain in the first place. It is very difficult to lose weight by trying to eat less energy than the body expends. Undereating requires substantial willpower which can be weakened by the presence of palatable foods and is counteracted by biological mechanisms such as increased hunger and a lower basal metabolic rate. In contrast, overeating occurs passively and is largely not compensated for by a reduction in appetite or later food intake. Dieting is not easily maintained in the long-term and is therefore not an effective weight control strategy. Consequently, a logical strategy for weight control is to adopt a highly satiating diet which will facilitate a reduced/adequate energy intake without increased hunger or overly restrictive eating. This review explores the available evidence which indicates that different foods/macronutrients influence appetite and food intake to different extents. The efficacy of sugar and fat substitutes for weight control will also be briefly discussed.

Measuring the satiating power of foods

Satiety refers to the transient, food-induced suppression of eating behaviour and hunger. The intensity and duration of satiety is governed by numerous interactions among sensory, cognitive, digestive and metabolic responses. This review will focus mainly on evidence obtained from relatively realistic studies in which human subjects have actually eaten and digested foods rather than studies in which pure nutrients have been infused directly into the gut or bloodstream. The most common experimental design used to compare the satiating effects of foods involves feeding subjects a fixed amount of a test food and then assessing the subjects' feeling of fullness at specific time points over a certain time period (usually 1-2 h) after which the subjects are presented with a range of foods from which they can eat freely. Both the degree of fullness over the fixed time period and the energy intake at the ad libitum meal reflect the satiating power of the test food.

Macronutrient oxidation and satiety

Previously, it was assumed that the body did not discriminate between fat, protein or carbohydrate in terms of supplying fuel for energy needs since their metabolism was thought to be freely interconnected. However, it is now known that the different macronutrients are not equally directed towards oxidation or storage and are not equally satiating. There appears to be a preferential order in which ingested macronutrients are oxidised which reflects the the body's capacity to store each nutrient (3, 7). Alcohol is the most actively oxidised fuel since it cannot be stored in the body and is essentially a toxin (8). Second in order of priority are protein and carbohydrate. The body's capacity for storing them is relatively limited and rapid changes in oxidation are an important regulatory mechanism for maintaining the balance of the body's stores. Fat oxidation has the lowest priority since there is no urgent need to adjust fat oxidation to intake since the body's fat reserves are so large that short-term gains or losses are relatively negligible (3). Experimental protocols which induce changes in substrate metabolism have shown that hunger and food intake are linked to the availability and oxidation of ingested nutrients. Data obtained from epidemiological studies, dietary surveys and interventions, and laboratory studies indicate that, with the exception of alcohol, the satiating powers of the macronutrients parallels the oxidative hierarchy in healthy, well-nourished subjects (protein>carbohydrate>fat) (9). After ingestion, alcohol is actively oxidised but does not suppress hunger or food intake. Generally, it is an additive source of energy and favours fat storage, particulary when consumed with high-fat foods (10). Each macronutrient class contains various subtypes which may have different profiles of absorption, oxidation and satiety. Although studies examining metabolic and satiety responses to pure nutrients provide important mechanistic data, practically relevant information must be based upon investigations of behaviourial and metabolic responses to normal foods under realistic environmental conditions.

Protein - a natural appetite suppressant?

Short-term studies have shown that meals containing moderate to large amounts of protein are highly satiating, especially when they are also rich in carbohydrate. Increasing a meal's protein content (31-54% of energy), whilst maintaining palatability and energy content, enhances feelings of fullness immediately at the end of the meal and over the next 2-4 h, after which ad libitum food intake may be reduced by 12-26% (11-15). Protein-rich foods have also been found to be more filling per kJ than carbohydrate- and fat-rich foods (16, 17), although in some cases this effect is not apparent unless the serving weights of the test foods are considered (18-20). Like carbohydrate-rich foods, protein-rich foods are more filling when they also contain 'intact' fibre (21) or when served in larger pieces (22).

The total protein content of the habitual diet appears to be a major determinant of satiation and total energy intake. During a recent dietary trial, subjects reported feeling much less hunger during a 2 wk high-protein weight-reducing diet (4.2 MJ/d) than when they were consuming an isoenergetic diet high in fat or carbohydrate (9). Similarly, dietary surveys indicate that total protein intakes correlate negatively with hunger (23) and total energy intake (24, 25).

The body has a relatively limited capacity for storing protein and protein balance is defended by acute changes in protein metabolism and food intake (26). Metabolic factors associated with the satiating power of high-protein meals include increased CCK and insulin secretion (27), increased protein oxidation (9, 28) and a slower rate of gastric emptying (11). The balance of certain amino acids may also be regulated as part of defending total protein status since dietary proteins with different amino acid profiles have been shown to influence food intake to varying extents. For example, beef has been found to be more filling than an equal amount of protein as chicken (29). Thus, the common practice amongst the weight-conscious of restricting red meat intake may be less effective in terms of appetite control. Increasing protein intakes above required levels in order to enhance satiety is not advisable since excess protein will be preferentially oxidised and may facilitate fat storage. Total protein intakes tend to remain relatively stable and have provided ≈ 11-14% of total energy intakes over the last 100 years in Western Europe, despite large changes in protein availability (30). In contrast, the proportions of energy derived from dietary fat and carbohydrate are larger and more variable and thus have a greater influence on satiety and total energy intake.

Carbohydrate compensation

A number of studies have shown that when healthy humans (children and adults, and restrained eaters) consume a carbohydrate-rich drink before a meal, they compensate for this extra energy by consuming less energy within the next 1-2 h. Compared to an equally sweet, low-energy solution, solutions of glucose, sucrose and fructose have reduced hunger and food intake at a meal 30-60 min later (31, 32). Similarly, plain yoghurt or tomato soup supplemented with maltodextrin supressed hunger and food intake at a meal 1 h later, whereas food intake was not suppressed after the equally palatable, low-energy controls (31) (Figure 1). In fact, the difference in the energy content of the high- vs low-energy test foods was fully compensated for by the reduction in later food intake. These findings support the hypothesis that changes in carbohydrate metabolism have a primary role in the short-term control of hunger and appear to contradict the belief that sugar stimulates appetite. However, highly controlled protocols were used and the subjects consumed a large amount of carbohydrate (50 g). In the context of normal foods, sweetness *per se* enhances palatability and may reduce the satiating power of a food (33). However, sweet, fatty foods induce greater energy intakes than sweet, low-fat foods (34).

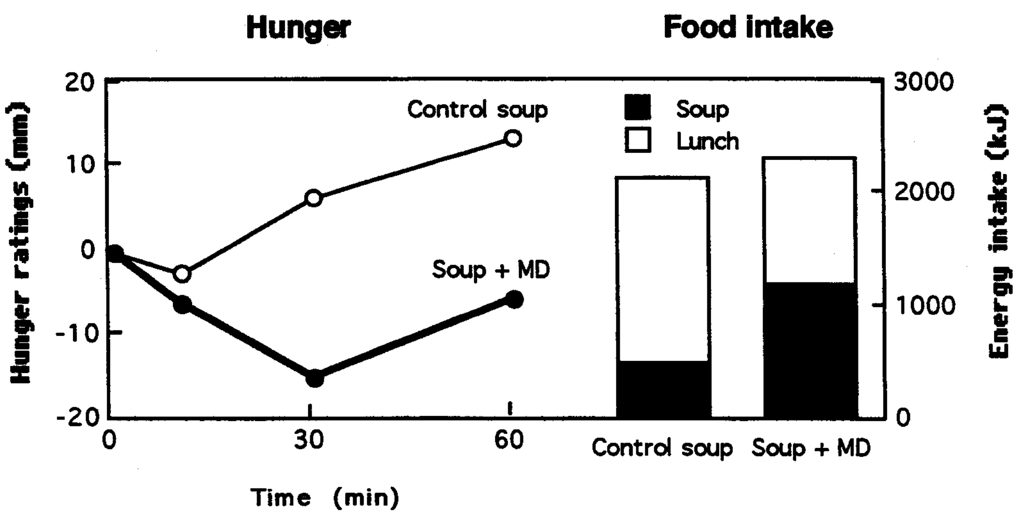

Figure 1. The effect of low- and high-carbohydrate soups of equal palatability and volume on hunger and ad libitum energy intake 1 h later (32).

Whether or not a reduction in energy intake is observed after a carbohydrate pre-load may depend on the time interval chosen between the consumption of the pre-load and the start of the test meal. For example, energy intake following a carbohydrate pre-load is more likely to be reduced if the next meal is eaten 2 h rather than 5 h later, after which the carbohydrate will have been largely absorbed and metabolised. Measurement of food intake after 1 h is sufficient for detecting compensation after pre-loads of glucose, sucrose or maltodextrin but may not be appropriate for more slowly-absorbed carbohydrates. For example, fructose suppressed food intake at a meal taken 2.25 h later but had little effect after only 1 h (32, 35). Therefore, the longer time required for satiety to peak may reflect fructose's longer absorption profile.

Carbohydrate digestion, glycaemia and satiety

Several tissues and organs, most notably the brain, have an obligatory requirement for glucose. Consequently, blood glucose levels are tightly regulated. Despite the crucial metabolic role of blood glucose, the body's capacity for glycogen storage is relatively limited. Therefore, glucose oxidation is closely adjusted to carbohydrate intake which optimises the body's ability to maintain adequate blood glucose levels (3). Between meals there is little fluctuation in the body's protein and fat reserves, whereas changes in carbohydrate stores are proportionally much greater. On this basis, it is logical to speculate that the return of hunger may be at least partly related to changes in glucose availability. The glucostatic theory proposed that central glucoreceptors (probably in the hypothalamus) detected the rate of peripheral glucose utilisation and modified hunger accordingly, ie hunger increases as the rate of peripheral glucose utilisation falls (36). Indirect evidence for a relationship between decreases in blood glucose levels or glucose availability is provided by a number of studies which have found that slowly-digested carbohydrate-rich foods which produce lower but sustained blood glucose responses are associated with greater satiety over the next 2-4 h than rapidly-digested foods (37-40). For example, as a carbohydrate-rich food, such as apples, oranges or wheat, is progressively refined, blood glucose and insulin levels rise while satiety falls in a step-wise fashion (41-43). Similarly, the addition of 2% guar gum to a glucose drink significantly reduced the rate of glucose absorption over the next 2 h and increased satiety (44). One study found that lunches with a high content of slowly-digested amylose starch produced smaller fluctuations in blood glucose and insulin levels and a greater degree of fullness over the next 6 h compared to two similar low-amylose meals (45). In this study, all four meals were rich in starch (57% energy) with moderate amounts of protein (13%) and fat (26%) and delayed the return of hunger to pre-meal values for over 4 h. Recent evidence suggests that the glycaemic impact of the overall diet may be inversely associated with total energy intakes. For example, rats maintained on a high-GI chow based on glucose or sucrose had higher energy intakes and body weights than rats consuming a low-GI chow with a similar macronutrient profile based on fructose or raw starch (46). Similarly, obese women lost more weight on a low-insulinaemic diet than on a conventional weight loss diet, despite consuming similar amounts of fat, protein and energy (47).

Collectively, these results imply that low-GI carbohydrate-rich foods are more satiating in the short-term than their high-GI counterparts. However, this is not a consistent finding and does not prove that lower, sustained blood glucose levels are directly responsible for enhanced satiety. Many low-GI foods are fibrous and bulky, which makes them more difficult to eat and enhances gastrointestinal distension. The slower rate of starch digestion and gastric emptying also prolongs the stimulation of chemical and mechanical receptors in the gut providing feedback signals to the brain (48). The glucostatic theory and other simplistic theories proposing that the depletion of a nutrient reserve stimulates the onset of feeding have lost favour. Postprandial increments in blood glucose and insulin levels do not necessarily directly predict the degree of glucose oxidation or storage in the liver/periphery (49-51). Nonetheless, a wide range of studies have consistently shown that carbohydrate- and protein-rich foods are more satiating that fat-rich foods. Under normal dietary conditions, carbohydrate metabolism in healthy people may have a more dominant effect on satiety than fat or protein metabolism since total carbohydrate intake usually accounts for the largest part of total energy intake. Thus, the total carbohydrate content of the diet may be a more important determinant of satiation and energy intake than the glycaemic impact of the diet.

Fat

In the past, fat was presumed to be satiating because it is energy dense and slows gastric emptying, whereas starch and sugar were believed to be fattening because they stimulated insulin release (52). These assumptions have since been shown to be incorrect. Much of the confusion regarding the satiating power of fat is directly due to the use of different experimental protocols since fat has a different effect on satiety depending on whether it is eaten or infused. In human subjects, oil infused directly into the stomach or small intestine, slows gastric emptying, increases feelings of fullness and reduces food consumption at the next meal. However, the infusion of fat directly into the circulation has no affect on gastric emptying or appetite indicating that the satiating effect of fat is not directly related to raised blood lipid levels *per se* (53, 54). Thus, under artificial conditions in which a large amount of fat is placed directly into the gut, the activation of gastrointestinal nutrient receptors and secretion of hormones, such as CCK, induce potent satiety signals before much of the fat has been absorbed (53).

The findings above suggest that the consumption of a large amount of fat should decrease appetite and subsequent food intake. Unfortunately, the infusion protocol does not mimic realistic postprandial conditions and greatly overestimates the satiating power of fat (55). Ingested fatty foods have been shown to be less filling than isoenergetic portions of protein- and carbohydrate-rich foods and result in higher energy intakes at meals consumed within the next 2-4 h (eg. 17, 56, 57) (Figure 2).

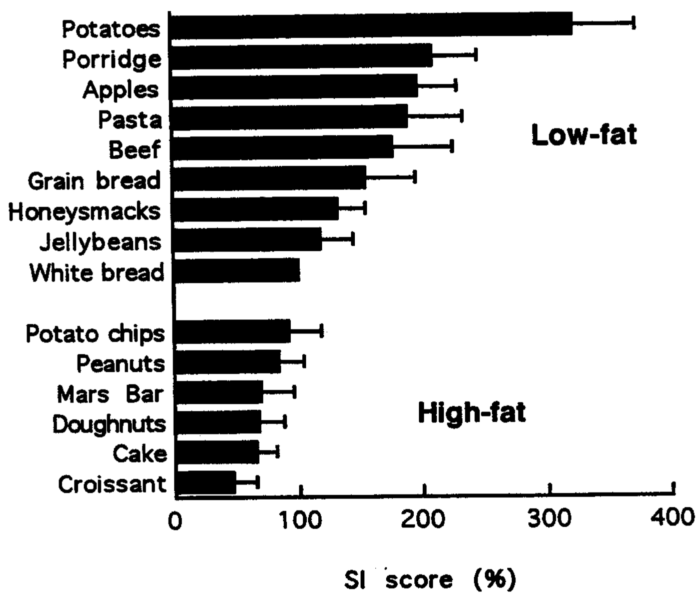

Figure 2. Mean ± SEM satiety index scores to 1000 kJ portions of common foods (17).

At the Human Appetite Research Centre of the University of Leeds, England, various groups of subjects (lean, obese and female dieters) have been tested in an experimental protocol in which they eat freely from a range of palatable foods that are either high in fat or carbohydrate until they are sufficiently full. Typically, the high-fat foods contain ≥ 50% of energy as fat and ≤ 30% carbohydrate (eg sausage rolls, chocolate, cheese, chips, biscuits), whereas the high-carbohydrate foods contain ≥ 55% carbohydrate as energy and ≤ 25% fat (yoghurt, jelly babies, sandwiches, swiss roll). In each study, the high-fat foods consistently induced significantly greater energy intakes (up to two-fold higher) than the high-carbohydrate foods (both sweet and savoury), even though the lean subjects tended to consume a smaller weight of the fatty foods (34, 57-62). Therefore, the fat content of the available foods was a stronger determinant of energy intake than the degree of hunger. Furthermore, the subjects did not compensate for the excess energy ingested at the high-fat meal by reducing fat or energy intakes at any stage over the next 24 h.

The passive overconsumption of fat is one of the most robust findings in appetite research. The secret addition of up to 50 g of fat to a meal also fails to produce an appropriate increase in satiety or a sufficient decrease in later energy intake (63, 64). A recent study examined the effect of covertly supplementing a standard breakfast with ≈ 1520 kJ of extra fat or carbohydrate (65). During the first 3 h after ingestion, the extra carbohydrate reduced hunger to a greater extent than either the standard or fat-supplemented breakfast. The subjects consumed significantly less energy after the carbohydrate-supplemented breakfast if the next meal was given 90 min rather than 4 h later, reflecting the duration of carbohydrate digestion and absorption. However, the fat-supplement did not increase satiety and the subjects did not eat less energy or fat at any stage over the next 24 h. It is likely that additional fat does not suppress hunger because it is absorbed slowly and is preferentially stored in adipose tissue rather than being oxidised (3). Meticulous calorimetry studies have shown that the addition of 50-106 g of extra fat to a mixed diet did not increase fat oxidation over the next 24 h in well-nourished humans, suggesting that most of the excess fat energy was stored not oxidised (66, 67). In contrast, carbohydrate-rich foods effectively stimulate carbohydrate oxidation and have a more 'immediate' inhibitory effect on appetite.

Fat-related dangers: palatability and energy density

Two features of fat-rich foods facilitate the rapid ingestion of a large amount of energy. Firstly, they are highly pleasurable and likely to be eaten quickly. Secondly, they are energy-dense so a lot of energy is contained within a small amount of food. However, palatable, energy-dense solutions of both carbohydrates (sweet and non-sweet) and fats have a stimulatory effect on appetite (75). A recent study specifically addressed the issue of whether humans overconsume a food because it is high in fat or high in sucrose. Healthy lean males were fed a low- or high-energy lunch followed 2 h later by the opportunity to eat freely from a selection of either high-fat, low-sucrose snacks (eg potato chips, sausage rolls) or low-fat, high-sucrose snacks (eg jelly babies, jam sandwiches, fruit yoghurt) (40). After either lunch, the subjects consumed >60% more energy when given the high-fat snacks compared to the comparable range of palatable, sweet snacks (Figure 3). The subjects actually ate a lower weight of the high-fat snacks but still consumed more energy due to the greater energy density of these foods. The results indicate that the passive overconsumption of energy from high-fat foods easily occurs whether a person is hungry or not. It is important to note that the carbohydrate-rich foods were highly palatable and were also eaten in relatively large amounts (up to 470 g). Less energy-dense carbohydrate sources such as fresh fruits, breakfast cereals and breads are not as palatable and would not be easily eaten in such large amounts.

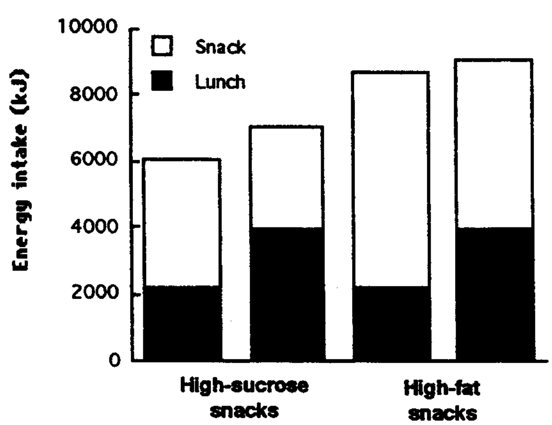

Figure 3. Mean energy intakes after 18 lean males ate either a low- or high-energy lunch and were presented 2 h later with a range of high-sucrose or high-fat snack foods.

Although sugar can enhance the palatability of fatty foods, fat rather than sugar is the greater determinant of excess energy consumption. However, the combination of carbohydrate and fat is highly pleasurable. Some energy-dense snacks, both sweet and savoury, (eg potato chips, chocolate, ice cream) are particularly resistant to satiation, ie they are 'moreish' and stimulate the desire to eat (17, 76, 77). This quality is particularly exploited in advertising campaigns and is even portrayed as a positive attribute promising pleasure and ensuring parents that their children will still be able to eat their dinner. These snack foods are generally eaten in addition to main meals and are associated with weight gain (78, 79). Sedentary people only have a very narrow margin between a balanced and an excessive energy intake. Therefore, the way in which these fatty foods are being advertised and sold (price, availability) warrants concern.

Sugar substitutes: sweetness without calories

In line with the popular belief that extrinsic sugar accounts for a large proportion of excess energy consumption, sugar substitutes have been widely added to the food supply since the 1980s. These products are assumed to facilitate weight control because of their lower energy content. However, by replacing carbohydrate, the kJ savings are often modest and the satiating power of the product may be reduced. Maintaining the level of sweetness without providing energy may in fact stimulate appetite. A number of studies have shown that pre-loads containing glucose, sucrose, fructose or maltodextrins exert good control over satiation, resulting in an accurate reduction in energy intake at the next meal (31-37). In contrast, non-caloric pre-loads made equally sweet with aspartame, saccharin or acesulfame K either increased or did not suppress hunger or food intake (31, 80, 81). Other short-term studies have produced conflicting results, largely due to the use of different experimental protocols (39). However, the overall conclusion is that sweetness without calories did not help people decrease their total energy intakes. These findings are consistent with metabolic evidence supporting a primary role for carbohydrate metabolism in the short-term control of hunger.

Epidemiological studies and controlled clinical trials have produced ambiguous results but the use of artificial sweeteners alone without other dietary and lifestyle modifications does not help people loose weight or prevent weight gain (82, 83). Some people believe that consuming an artificially sweetened beverage in place of a regular soft-drink gives them some caloric freedom to indulge in larger servings of their favourite foods. This compensatory behaviour has also been observed under experimental conditions when subjects have known about the energy content of either low-sugar or low-fat test foods (84, 85). Clearly, some degree of cognitive restraint and a combination of dietary and behaviourial modifications (fat and total energy reduction, regular physical activity) are essential for weight control in modern, sedentary lifestyles.

The previous belief that sugar intake is strongly related to weight gain has not been substantiated by recent epidemiological studies. Overweight people tend to eat less sugar (and starch) but more fat than lean people (eg 86, 87). This phenomenon has been called the 'sugar-fat seesaw' and suggests that a moderate sugar intake (natural and added) makes a low-fat diet more palatable and able to be maintained in the long-term. Common foods associated with 'carbohydrate craving' and weight gain have been wrongly labelled as sugar-rich foods when in fact they contain a high proportion of fat (eg biscuits, chocolate, pastries, ice cream). Other studies have shown that obese subjects prefer the taste of higher fat levels in common foods such as milk, scrambled eggs, mashed potatoes, tuna, and snack foods (88, 89). This increased preference for fat may be due to the habitual consumption of fat-rich foods rather than an inherited behavioural trait (90). On average, refined sugar accounts for only 11% of total energy intake, whereas fat accounts for ≈ 35-40% of energy intake. A small reduction in fat intake would correspond to a much larger decrease in kJ intake and would be easier to achieve than a strict avoidance of all added sugars.

Are fat substitutes effective for weight control?

Dietary surveys and interventions have shown that high fat intakes are associated with higher total energy intakes and greater adiposity (91-93). In fact, weight gain appears to be more strongly related to dietary fat intake than total energy intake (94). Several experimental trials have shown that strict adherence to a low-fat diet (15-25% of energy) results in a gradual loss of body fat under controlled (95-98) and free-living conditions (94, 99). Although, in some cases, the subjects gradually increased their energy intakes during the very low-fat diet, total energy intakes still remained lower than during the high-fat condition (97, 98). Furthermore, spontaneous weight loss has also been observed in large-scale trials in which fat consumption was reduced in order to decrease serum cholesterol levels (100-102). It must be emphasised that these low-fat diets were based on foods with a high fibre and water content and a low energy density, such as cereals, fruits and vegetables, which are more difficult to eat, generate greater gastric distension and can satisfy appetite at a much lower energy level than high-fat foods (95).

As with artificial sweeteners, evidence from short-term studies questions the efficacy of fat-reduced foods for weight control. Unfortunately for sedentary people, humans appear to detect and compensate more readily for decreases in energy intake than increases in energy intake (103). Several laboratory studies have shown that when subjects are free to consume from a range of foods with various energy densities they subsequently increase their food intake after consuming a meal whose fat content has been covertly reduced (103-107). Total day energy intakes remained constant but total fat intakes were reduced. Therefore, fat substitutes can reduce fat intakes and increase carbohydrate intakes without changing total energy intakes or compromising satiety (107). It is important to note that the subjects in these studies were lean unrestrained eaters who were not trying to lose weight and may have more sensitive energy regulatory systems than obese subjects and restrained eaters (108).

Controlled low-fat dietary interventions have successfully induced weight loss by maintaining their subjects on foods with a low-energy density (eg fruits and vegetables), thereby, increasing the volume of food needed to maintain energy intakes. Whether new low-fat products which are still highly palatable and relatively energy dense (eg fat-reduced ice cream, yoghurt, biscuits) can maintain satiety and facilitate weight loss remains to be seen. People need to be educated about the correct use of 'lite' foods because of the common misperception that larger than normal portion sizes will still contain fewer kJs (85). Nutritional panels on the labels of 'lite' foods should include a measure of the energy density of the product. Parallels can be drawn between the serious health effects of smoking and high fat, weight-inducing foods. Warning messages may be appropriate for both. Mandatory reductions in the fat content or a 'sin tax' should be considered (109). Recent dietary education messages have strongly advocated fat restriction as the basis of achieving weight control. However, both total fat and energy intakes need to be moderated since weight gain is possible on a high-carbohydrate diet when excess energy is consumed.

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