Role and benefits of carbohydrate in the diet: key issues for future dietary guidelines[1-3]

Jules Hirsch

ABSTRACT There is now widespread advocacy for a reduction in fat intake. Furthermore, there is little evidence that an increase in protein intake would be advisable. Therefore, a greater proportion of carbohydrate energy in the diet has become a central tenet of current dietary advice. A careful examination of the benefits of a "high"-carbohydrate diet must therefore occupy our attention. Three aspects of the role of carbohydrate in the diet will be considered: *1*) the role of carbohydrate in the control of food intake in humans, *2*) the effect of carbohydrate on energy metabolism as measured by long-term feeding experiments in small numbers of human subjects, and *3*) whether a large carbohydrate intake leads to increased lipogenesis in humans. *Am J Clin Nutr* 1995; 61(suppl):996S–1000S.

KEY WORDS Diet, carbohydrate, role, benefits, guidelines

Introduction

Evolutionary and historical perspectives lend depth to a consideration of the role and benefits of carbohydrate in human diets. The data presented here on the diet of simians is derived completely from the findings and observations of Milton (1). The extrapolations I will make, however, are possibly unwarranted and for these I take credit.

Roughly 60 million y ago in the Cretaceous Period, the last period of the Mesozoic Era, forests spread across the surface of the earth. At that time, or shortly thereafter, at the beginning of the Paleocene Epoch, the ancestors of current simians became tree dwellers. Trees provided not only a protective home for these ancient animals, but also were their major source of nutrition. At the lower levels of the trees, young leaves provided a diet with some protein, but the carbohydrate that was available was combined with tough fiber. On the other hand, the upper surfaces of the trees, the arboreal canopy facing the sun, were richly endowed with the growing parts of the plants as well as flowers, berries, and fruits. As is well known to every indoor gardener, the flowering parts of plants and thus the products of the flowers are most concentrated in the sunniest areas. Here the foodstuffs available to the simians were fruits with readily accessible and relatively easily digestible carbohydrates; the upper leaves contain much less fiber and less protein than the leaves at lower levels. It is suggested that the relative abundance of leaves lower down in the forest canopy permitted the development of monkeys that did not need to forage widely, and who subsisted on the high-fiber, carbohydrate-containing leaves. Some animals, such as the modern colobine monkey, developed an alkaline forestomach with a marked resemblance to the gastrointestinal system of ruminants. The forestomach contains bacteria that digest cellulose and thereby maximize the nutritional possibilities of a leaf diet. On the other hand, those animals developing at the tree tops had to forage more widely for fruits and berries and also had to develop the cognitive apparatus for remembering where these are located in the trees. Their diets, rich in simple sugars, permitted the sustenance and rapid development of a large central nervous system, an obligate consumer of sugar, which was needed for memory, sight, and all the sensory modalities required for wide-ranging foraging in the forest canopy.

Modern-day derivatives and at least partial exemplars of these evolutionary differences are the spider monkey and the howler monkey. Both are of similar weight, ≈6–8 kg, but the spider monkey, which consumes a diet that is ≈72% fruit and only 22% leaves, has a brain size of 107 g, whereas the howler monkey, the more sedentary dweller who lives lower in the trees, has a diet of 48% leaves and 42% fruits and half the brain size (50.3 g). The day range of the spider monkey is estimated as being 915 m compared with the day range of the howler monkey of only 443 m.

One can imagine, therefore, that animals who could carefully search through the tops of trees with a developed brain, learning and remembering which fruits were bitter or poisonous and rapidly localizing safe and tasty fruits and berries, might be the forerunners of the relatively large-brained creatures that much later descended from the trees to become hunter-gatherers.

Ancestors closer to us in evolutionary time and which were no longer dwelling in tree tops had the pressing dietary problem of an inconstant food supply. The search for food away from the leafy forests led to the consumption of a greater variety of foodstuffs, but also to the peril of long periods of great scarcity. The storage of fat made either from ingested sugars or by direct ingestion of fat must have been an important metabolic adaptation in shaping our ancient diets. The clear metabolic utility of fat, whether ingested moment-to-moment

[1] From the Laboratory of Human Behavior and Metabolism, The Rockefeller University, New York.

[2] Supported by NIH grant 2 MO1 RR00102.

[3] Address reprint requests to J Hirsch, The Rockefeller University, 1230 York Avenue, Box 310, New York, NY 10021–6399.

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or metabolized from adipose tissue, is the sparing of glucose for energy needs. In the starvations faced by ancient humans, dietary fat and stored fat came to the rescue, sparing sugar for central nervous system function. Even the metabolic adaptations that we now experience on a diurnal basis at night, when we draw on supplies of fat to spare glucose for our ceaselessly active and dreaming central nervous systems, are echoes of that past in which supplies of carbohydrate were scarce and intermittent.

Examining our dietary histories in more recent time yields observations that are studded with conjecture and uncertainty but that may nevertheless be of interest in our understanding of the role of carbohydrate in the diet. The analysis I present is based on that of Eaton and Konner (2). Using their scholarly treatment of the subject, I have taken the liberty of making some further guesses as to what changes have occurred in our diet as we moved from the hunter-gatherer through the more recent agricultural period of recorded history of some 6000 y and finally into the present.

Figure 1 shows an estimate of energy consumption per day. Note that time is on a logarithmic scale. The jagged curves from 1 million y onward are my effort to emphasize the intermittence of the food supply. Obviously, the presentation here can only be a reminder of the intermittent supply because the true scale would show so many repeated episodes, even on an annual basis, that it would appear more like a brush border or a solid bar. An important point to note is that with the coming of agricultural practices, it is likely that many in the population became relatively more sedentary and hence the energy demand was reduced. Furthermore, periods of starvation became fewer when the food supply became more predictable as the result of the growing of grains and the domestication of animals. In our most recent period, the past 150 y, humans have become taller and fatter and there is an associated increase in energy consumption.

But how about carbohydrate consumption over time? **Figure 2** is a guess. It would be reasonable to assume that in the early days of hunting and gathering, carbohydrates were a smaller fraction of the diet than when grains and farm products became available. **Figure 3** shows the likelihood that protein intake declined with the coming of agriculture and a higher carbohydrate intake. That this is likely to be the case is borne out by the relatively small stature of humans for several thousand years of recorded history, with only recently a sharp increase in height. Equally significant changes are suggested by **Figure 4**. Fat intake may have been high when animals were being consumed as the major element of the diet. A reduction during the agricultural period is shown, followed by a remarkable increase in fat intake since the onset of the industrial revolution.

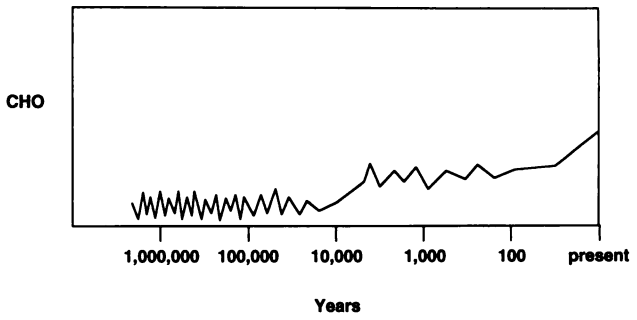

FIGURE 2. Estimated changes in carbohydrate consumption in humans over time.

What does this mean in terms of our present food consumption patterns and their role in health and disease? We have a large central nervous system thirsting for simple sugars. It would appear, then, that the search for sugars via sweetness, the taste marker for sugars, is a fundamental "wired in" aspect of our food selection. The uncertain availability of all foods in our past also makes us searchers for energy. So a second heritage is the urge to consume energy and in its most efficient and dense form, fat. There are undoubtedly many other factors that generate specific hungers or appetites, but underlying all is the need for an adequate glucose concentration in the plasma, without which unconsciousness and death supervene quickly, and alternative sources of energy to protect the precious, simple sugars. This analysis of the utility of sugars in the evolution of the brain could have been made in similar fashion for the evolution of muscle. With physical activity, however, there is the option for trained compared with untrained muscle, and red compared with white fiber, to use primarily fatty acids or glucose for metabolism. With the brain there is no such option, with the exception of ketones, which play a role in chemical rescue only during starvation.

Until recently, our dietary choice was made by resolving two vectors; the first vector derives from our innate "tendencies" as a result of our evolutionary history. It is reasonable to assume that foremost among these is a yearning for sweet taste, which is a marker of rapidly available carbohydrate, but also a yearning for energy. The other significant vector making our choice

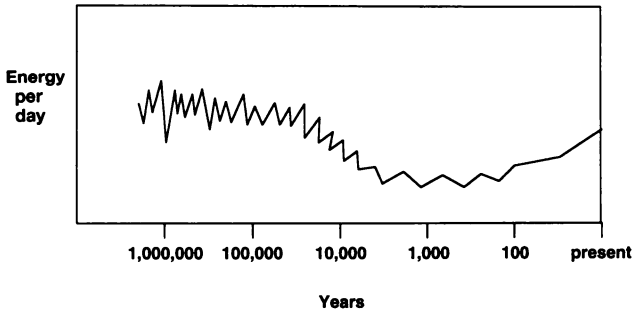

FIGURE 1. Estimated changes in energy needs in humans over time.

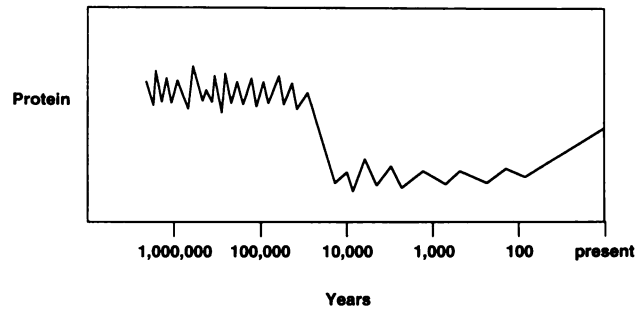

FIGURE 3. Estimated changes in protein consumption in humans over time.

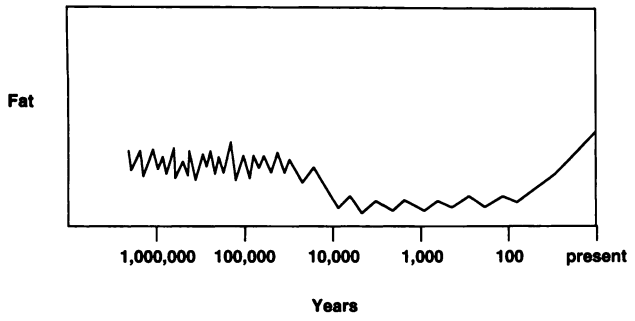

FIGURE 4. Estimated changes in fat consumption in humans over time.

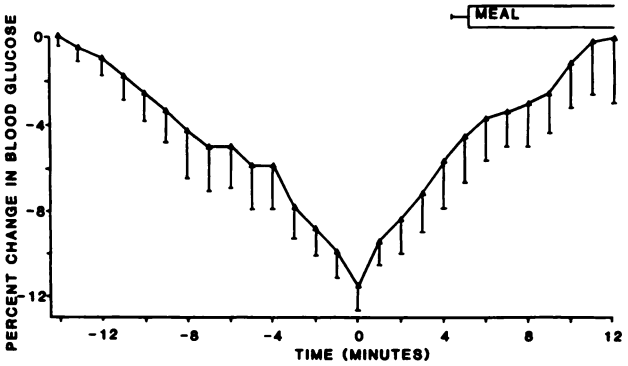

FIGURE 5. Changes in blood glucose concentration before feeding in rodents. From the work of Campfield and Smith (3).

is simply availability. This changed ≈150 y ago. Since the beginning of the industrial revolution, large segments of the Western world have had limitless supplies of sweet foods, as well as fat, the most efficient means of consuming energy. There probably never has been a time in our history when dietary practices have changed so radically as they have in the past 150 y.

A third vector, which in recent decades has entered the scene, is the consideration of what is healthful. With longer lives and a prevalence of illnesses that reflect our greater longevity, we now wish to modify our dietary choices in the belief that diet can play a role in sustaining health. Current information strongly favors the concept that lifelong diet is related to many common diseases. From many lines of evidence it is believed that a reduction in fat intake, and perhaps a reduction in total energy intake, would be beneficial for health. Data being accumulated in many laboratories will help to refine these broad dietary recommendations into more detailed dietary prescriptions for health, which may vary on an individual basis as genetic and other factors that contribute to individuality are better understood. Some recent contributions to this endeavor have been from my own laboratory.

Signals for food intake

The above discussion supports a close relation between glucose and central nervous system function. It is often reasoned that the complexity of learning and cognition related to human food intake make it very unlikely that there are simple chemical signals for food intake in humans. Whatever is "wired" is likely to be overwhelmed and invalidated by learned behaviors and social factors. Thus, it may be reasoned that single clinical entities cannot be major factors in the regulation of food intake in humans, as may be the case in some animal models. Members of my laboratory, in collaboration with Campfield and Smith (3), have performed experiments examining the possibility that blood sugar concentrations in humans can function as initiators of feeding behavior. **Figure 5** is taken from a publication of Campfield and Smith (3) that examined the relationship of minute-to-minute blood glucose concentrations to food intake behavior in rats. They found, as shown in this curve, that a 10–15% decline in blood glucose before the initiation of a meal is a common occurrence in rats. Interestingly, meal intake does not begin at the nadir but rather when the curve is returning to the initial level after the decline. There is evidence that these declines may be related to small spikes of plasma insulin secreted under the influence of an intermittent parasympathomimetic discharge. This brings up many interesting questions concerning the neural sensing of blood sugar concentrations. Is there a combined hormonal-neural mechanism whereby the status of glucose storage is sensed by an internal insulin challenge and food intake is "decided" on the basis of the insulin effect? I can now report to you that my colleague, Michael Rosenbaum, working with Smith and Campfield, has recently shown that this phenomenon occurs in humans as well (4). Subjects were admitted to the Clinical Research Center of The Rockefeller University Hospital and in a careful experimental design, excluding time and other cues relevant to food intake, were allowed to make estimates of their hunger and to request their meals. Precisely similar alterations in blood glucose occurred as those seen in rats. Meals were requested soon after spontaneous, small declines in plasma glucose concentrations.

How important these alterations are in determining food intake and food choices in humans remains unknown. Yet, it is a surprise that given the complexity of the factors that compose food choice and meal initiation, a robust mechanism of this type remains operative and easily discernible. The clear demonstration of this coupling between blood glucose concentrations and food intake in humans and its mode of operation will undoubtedly stimulate further study of how carbohydrate affects appetite and food intake. Further experimental details of these findings are being prepared for publication.

Energy value of carbohydrate

My colleagues and I have examined data obtained on 16 human subjects who received liquid diets of precisely known composition during prolonged studies at The Rockefeller University Hospital (5). For a variety of experimental purposes, the fraction of energy obtained from carbohydrate varied widely. In some instances, a diet with 75% of energy from carbohydrate was compared in the same individual with a diet containing 15% of energy from carbohydrate. In these individuals with a "clamped" intake, which was sufficient in amount to maintain body weight, we could find no evidence for alterations in overall energy need that depended on the percent carbohydrate in the diet. This is shown in **Figure 6** in a 64-y-old nonobese

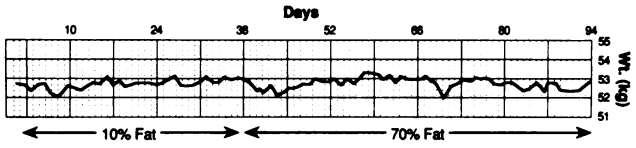

FIGURE 6. Precise equienergetic feeding of a human subject on very high- and low-carbohydrate diets with no significant change in body weight over a period of > 13 wk. From work by Leibel et al (4).

individual who was fed a diet that changed from 75% to 10% carbohydrate over a period of many days. The fact that body weight remained sufficiently constant suggests that alteration in fat storage during these times is unlikely. Energy need remained unchanged at 7322 kJ/d in this individual, despite the extreme change in carbohydrate intake. This is important to consider because diets high in carbohydrate may lead to transient changes in thermogenesis or other aspects of metabolism that make them less efficient sources of energy. It would appear that in the long term, kilojoule for kilojoule, fat and carbohydrate are equally effective at maintaining body weight. Of course, with a free choice of solid foods, a high-carbohydrate diet might lead to other effects such as the selection of a diet with less energy. This was not tested in this experiment.

Is there lipogenesis from carbohydrate in humans?

Under ordinary circumstances in which ≈40% of energy is consumed from fat, there is probably relatively little lipogenesis from carbohydrate. This statement is based on the knowledge that with usual diets, adipose tissue lipids reflect the fat composition of ingested fat. If there was significant lipogenesis, one would anticipate that adipose tissue would reflect lipogenesis by showing a composition characteristic for fats produced by lipogenesis compared with those in the diet. This is not the case. In fact, we suggested many years ago that adipose tissue fatty acid composition reflects dietary fat. **Figure 7** shows our best estimate 30 y ago of the amount of unsaturated and saturated fats in the average American diet and also the average adipose tissue composition. On the far right, we see the effects of feeding an individual a corn oil–rich diet, when 40% of energy was obtained from corn oil. The 50% linoleic acid content of the corn oil markedly alters adipose composition over a period of time. If there had been significant lipogenesis from carbohydrate, a "harder" fat would have been deposited, one less rich in linoleic acid that could not be synthesized from carbohydrate by humans. Hence, these data speak against significant long-term lipogenesis from carbohydrate.

There is a circumstance in humans, however, in which abundant lipogenesis from carbohydrate appears to occur regularly—the last trimester of pregnancy. Because placental transfer of free fatty acids is much more sluggish than placental transfer of glucose, there is little resemblance between newborn fetal fat and the fat of the mother. Rather, fetal fat appears to be made largely, if not exclusively, from carbohydrate. So, there is at least one time in life when we do make a lot of fat from carbohydrate and when that fat is saturated or monounsaturated fat. It is likely that membranes and other vital structures that

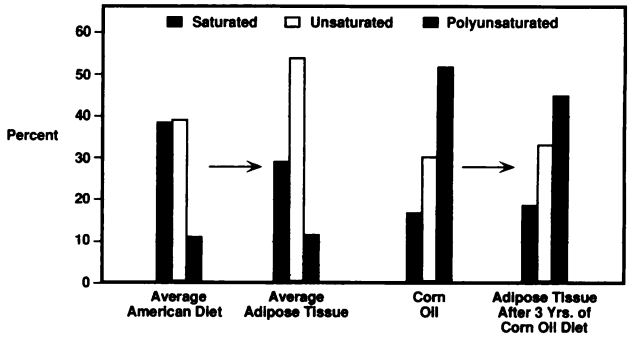

FIGURE 7. The similarity of fatty acid composition in the diet and adipose tissue of humans. Data for average American diet from the US Department of Agriculture, 1955.

are in equilibrium with pools of stored fat share the same fatty acid composition. Is this in any way detrimental to the fetus? This composition of fat stores changes rapidly when food intake of a fairly high-fat diet begins, and the fat of maternal milk or of a formula diet rapidly makes its imprint in fetal lipid compartments. Note, however, that the vast bulk of central nervous system development occurs antenatally, or in the earliest perinatal time when a very-high-carbohydrate diet is of necessity being fed because of the limitations of placental transfer of fat. We know that premature infants can develop on a diet that is different from that provided by the placenta, because this is what we feed them. It appears then, that the ordinary high degree of carbohydrate feeding in utero is not absolutely essential. Yet, the neural susceptibility of premature infants and our incomplete understanding of the relationship of diet to neural development in these early stages in life, suggest that judgment as to what is optimum carbohydrate feeding for newborns and in particular prematurely born newborns, might be periodically revisited.

The next question, however, is whether anything like this occurs in adult humans. Are there episodes of lipogenesis of this degree in adults? To study this phenomenon, my colleagues Hudgins et al (6) admitted patients to our Clinical Research Center and provided them with formula diets of widely ranging amounts of carbohydrate. The technique they used was to feed a dietary fat with a composition very similar to that of adipose tissue. In this circumstance, plasma very-low-density-lipoprotein (VLDL) triglycerides have fat derived either from adipose tissue or from the diet, however, because both sources of fat are the same in composition, the VLDL triglycerides should have a composition equal to adipose tissue unless there is de novo synthesis of fat from carbohydrate. The experimental manipulation in this study was to feed different amounts of carbohydrate and to determine at what level of carbohydrate intake lipogenesis becomes evident in the fatty acid composition of VLDL triglycerides by a decline in the linoleic acid concentration, ie, through dilution with newly synthesized fatty acids devoid of linoleic acid. With a diet in which 10% of energy is from fat, and with fatty acid composition matched to that of adipose tissue, there is marked lipogenesis. The VLDL triglyceride comes to resemble fetal fat composition because it is enriched by the fatty acids characteristic of those made from carbohydrate. Under these condi-

tions of very-low-fat or high-carbohydrate feeding, plasma triglyceride concentrations also rise and often stay elevated for long periods of time.

Hudgins et al (6) also made other measures of lipogenesis in these same individuals, using [^{13}C]acetate incorporation into VLDL triglyceride palmitate. The data that they accumulated were concordant with the findings described above, namely, there is lipogenesis from carbohydrate in adult humans when high amounts of carbohydrate are fed.

It may be considered somewhat distressing to note that as less fat and more carbohydrate is fed, there is production of endogenous saturated fat, which might be unwanted. However, there are several important mitigating factors. The first of these is that when the carbohydrate is fed as complex sugars rather than as simple sugars, this effect is greatly diminished. It remains uncertain how much individual variation there is, ie, what percent of carbohydrate feeding will induce this lipogenesis in each individual and furthermore, how much complex carbohydrate or starch is required to reduce lipogenesis produced by simple or refined sugars. These are important areas for study in designing diets optimum in amount and type of carbohydrate.

These observations lead me to the conclusion that although a reduction in fat intake is very likely a worthwhile dietary recommendation, we must continue studies to refine that recommendation. The ratio of complex carbohydrate or starch to simple sugar, and individual variation in response to a high-carbohydrate diet, may demand that we tailor the dietary prescription on the basis of further information. The close role of simple sugars to the development of the central nervous system and its function also demand further attention to dietary effects early in life. We must surely eat to satisfy our metabolic needs and our innate drives, but the ingenuity of food technology can help us to make a better match with these needs and drives than has been the case for most of the past 100 y. Satiation of the desire for sweetness or the sensation of fatness in foods can, to some degree, be engineered by the food industry. It seems reasonable that as we accumulate further knowledge, selections can be made that both satisfy our needs and desires and lead to a more healthful outcome than has been the case with foods we have elected to consume since the onset of the industrial revolution.

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