

The Winter Meeting of the Nutrition Society was held at the Royal College of Physicians on 27 January 1999

Symposium on ‘Social and environmental influences on diet choice’

What are the major correlates of macronutrient selection in Western populations?

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In order to better understand the factors that may influence and regulate the intake of the macronutrients carbohydrate, fat and protein a 7 d diet diary technique was employed to study eating behaviour in the natural environment of free-living human subjects. In general, factors that promote energy intake tend to promote fat and protein intake to a greater extent than carbohydrate intake. This increased intake occurs as the result of: environmental factors such as social facilitation and the time of day, week or lunar phase; subjective factors such as hunger and elation; individual difference factors such as obesity, restraint and ageing. There are indications that the intake of macronutrients is regulated by negative feedback systems. In the short term, the amount of protein remaining in the stomach at the onset of a meal appears to have a restraining effect on intake, especially protein intake. Over several days, macronutrient intake appears to be affected by a nutrient-specific delayed negative feedback. Protein intake during 1 d is negatively associated with protein intake 2 and 3 d later, while carbohydrate intake is negatively related to later carbohydrate intake, and fat intake to later fat intake; both peaking after a 2 d delay. Studies of the intakes of twins suggested that many aspects of the control of macronutrient intake are influenced by inheritance; these factors include the overall amounts ingested, the before-meal stomach contents and the responsiveness of the subject to the negative impact of the stomach contents. The results indicate that macronutrient intakes are regulated by multiple persistent processes that are to a large extent inherited.

Eating behaviour: Meal pattern: Macronutrient intake: Hereditary influence

At its most fundamental, diet selection is the selection of macro- and micronutrients. These nutrients are ingested in a wide variety of presenting forms. However, the types of foods available, preparation techniques and affordability of food types vary greatly between cultures and even within cultures during different times of the year. As a result, an understanding of the processes involved in the selection of particular food items would be highly culturally specific. Also, the physiological system has evolved to operate in order to produce adequate nutrition in the face of varying available diets. Hence, the present paper will be focused not on the superficial layer of intake regulation or item type selection, but on the deeper layer, the controls and consequences of macronutrient selection.

The macronutrients carbohydrate, fat, protein and alcohol are the primary components of foods and are oxidized for

energy. The total food energy ingested is the arithmetic sum of the energy supplied by each of these nutrients. It is possible that the system is designed simply to regulate the total food energy ingested, regardless of macronutrient source. On the other hand, the system could involve a separate regulation of each of the component nutrients. There have been a large number of laboratory studies investigating these issues (for example, see Mela, 1997; Thibault & Booth, 1999). However, the regulation of the intake of individual macronutrients by free-living human subjects has received little attention. It is relatively easy to demonstrate that a nutrient is regulated in a tightly-controlled laboratory situation where there are few other factors operating to influence intake. However, it is much more difficult to demonstrate such control with individuals in their varied complex normal environments, in which they

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ingest a heterogeneous diet of which the composition is to some extent determined by the individual, and to some extent by other individuals (de Castro, 1996, 1997c).

In order to study macronutrient regulation in free-living human subjects we have employed a 7 d dietary diary technique (de Castro & Kreitzman, 1985; de Castro, 1987a,b, 1988a, 1990, 1991a,b,c, 1993a,b,c,d, 1994a,b, 1995a,b, 1996, 1997a,b, 1998a,b; de Castro *et al.* 1986, 1990, 1997; de Castro & Elmore, 1988; de Castro & de Castro, 1989; Elmore & de Castro, 1990, 1991; de Castro & Brewer, 1992; Redd & de Castro, 1992; Henson *et al.* 1993; de Castro & Pearcey, 1995). The participants record (in a small pocket-sized diary) each meal, where and when the meal occurs, exactly what they eat or drink, how it was prepared, their subjective states, and the number and nature of other people eating with them (for a discussion of the validity and reliability of this technique, see de Castro, 1994b). The data collected were analysed to investigate the factors and conditions that promote or inhibit the ingestion of individual macronutrients.

Factors that are correlated with macronutrient intake

Subjective state correlates

The subjective state of the individual can influence overall intake and the intake of the macronutrients. Self-rated hunger at the beginning of the meal is related to meal size (de Castro & Elmore, 1988). With increasing subjective hunger there is an increase in the intake of each of the macronutrients (Fig. 1(a,b)). However, the proportions of fat and protein increase while the proportion of carbohydrate decreases. Another subjective state that we requested subjects to self-report in the diet diaries was depression *v.* elation. The greater the elation level (lower depression) the more that tends to be eaten in the meal (Fig. 1(c,d)). This increase occurs with all three macronutrients. However, as with hunger self-ratings, the proportions of fat and protein increase while the proportion of carbohydrate decreases. Hence, meals eaten when either hungry or elated tend to be high-fat and high-protein meals.

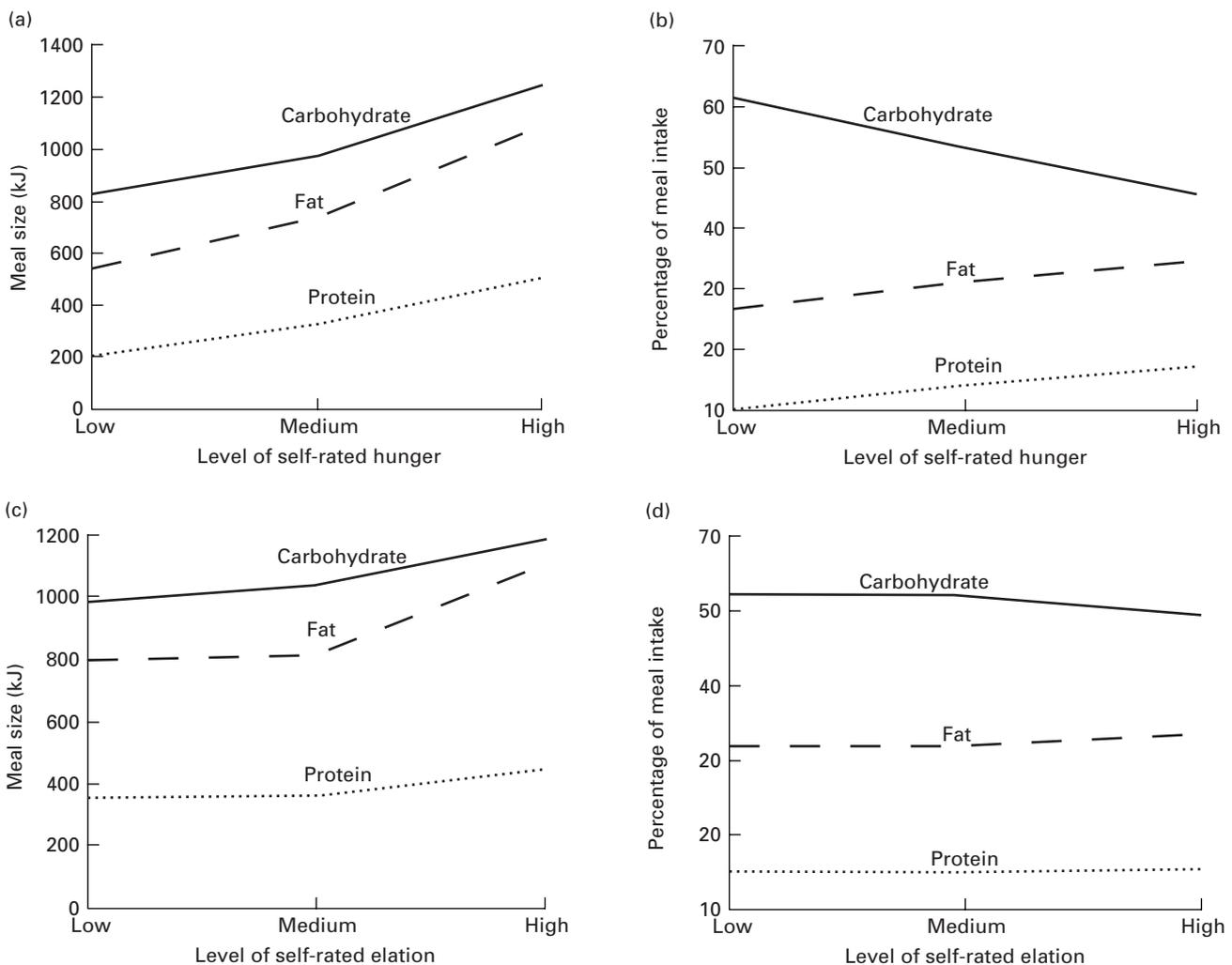


Fig. 1. Mean meal intake (a,c) and the proportion of the meal intake (b,d) of carbohydrate (—), fat (- - -) and protein (· · ·) ingested by participants at low, moderate and high levels of self-rated hunger (a,b) and at low, moderate and high levels of self-rated elation (c,d).

Social correlates

One of the most powerful influences on the amount ingested in a meal is the influence of the presence of other individuals at the meal. The more individuals that are present, the more that will be eaten in the meal (de Castro, 1990, 1991a, 1994a, 1995a, 1997a,b; de Castro & de Castro, 1987; de Castro & Brewer, 1992; de Castro *et al.* 1990; Redd & de Castro, 1992). In addition to the overall amount, the proportion of the macronutrients ingested also appears to be affected. Meals eaten with other individuals have a significantly lower proportion of carbohydrate and a higher proportion of fat than meals eaten alone (de Castro & de Castro, 1987).

Rhythms

Over the course of the day there is a considerable and fairly regular fluctuation in intake, with the individual ingesting larger meals separated by shorter intervals as the day progresses (de Castro, 1987a). This diurnal intake rhythm is different for the macronutrients, with morning ingestion tending to be relatively high in carbohydrate, midday intake relatively high in protein, and evening intake relatively high in fat (de Castro, 1987a). These effects appear to be present across cultures since a similar picture emerges for the French, Dutch and North Americans (de Castro *et al.* 1997). Hence, the time of day appears to be a significant influence on macronutrient selection.

Over the course of the week there is also a regular fluctuation in intake, with both total daily intake and meal size increasing at weekends (de Castro, 1991c). This increase is accompanied by increases in the intakes of all macronutrients. However, the intakes of fat and alcohol are heightened to a greater extent at weekends than carbohydrate and protein. There is even a small fluctuation in intake with the lunar cycle, with larger meals containing more fat and less alcohol being consumed with the full moon (de Castro & Pearcey, 1995). Finally, there also appears to be a seasonal rhythm in intake. During the autumn there is an increase in overall intake that primarily results from an increase in carbohydrate in comparison with the other seasons (de Castro, 1991b). Hence, weekends and a full moon tend to promote fat intake while the autumn season tends to promote carbohydrate intake.

Individual differences

There are large differences between individuals in the amounts and proportions of macronutrients ingested. One of the factors producing these differences is obesity. The relationship between macronutrient intakes and the BMI is presented in Fig. 2. As obesity (BMI) increases the proportions of fat and protein in the diet increase while the proportion of carbohydrate decreases. This relationship has been reported by other workers (Kulesza, 1982; Miller *et al.* 1990). Another factor is the active restraint of intake

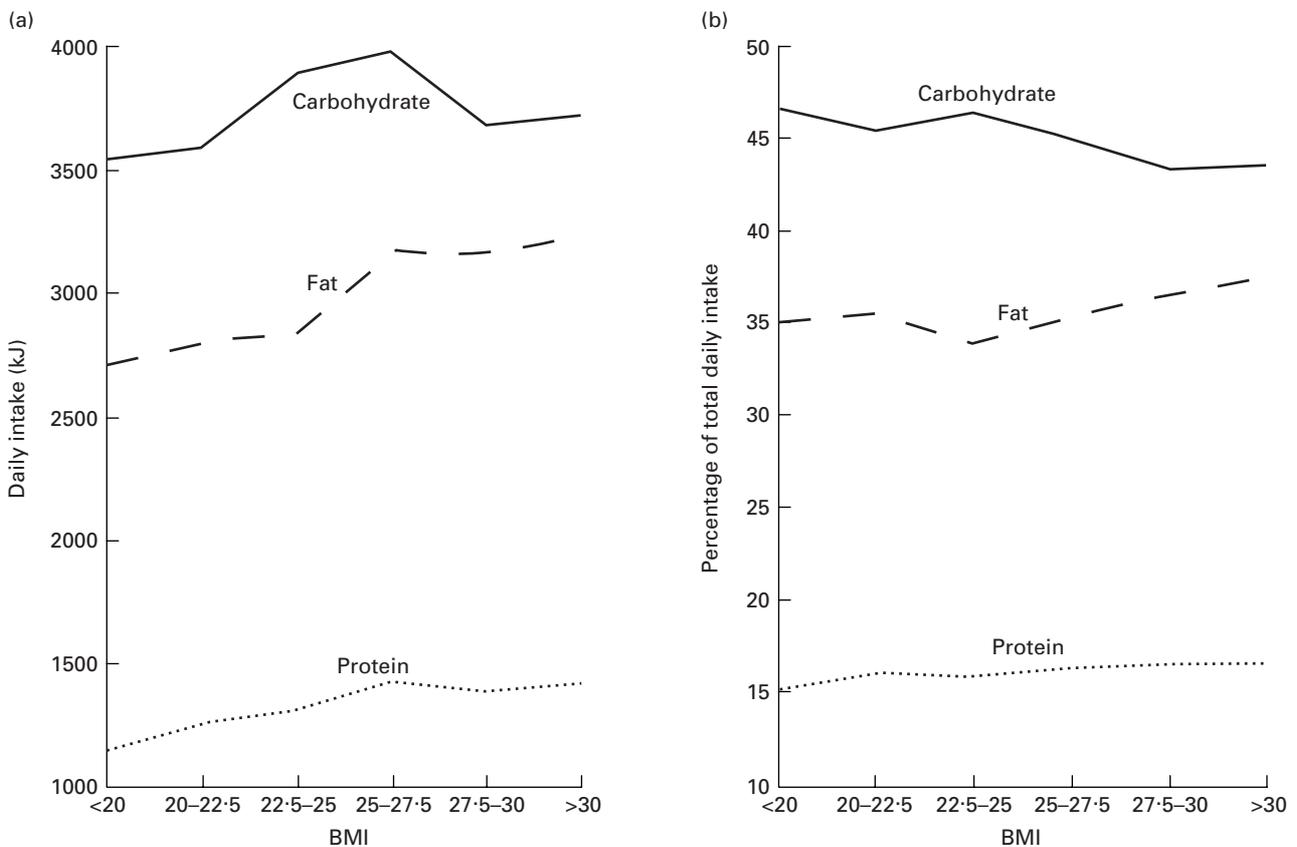


Fig. 2. Mean daily intake (a) and the proportion of daily intake (b) of carbohydrate (—), fat (---) and protein (···) ingested by participants at different levels of BMI.

by the individual. Individuals who score high on restraint eat significantly less than less-restrained subjects, and do so particularly by reducing fat and carbohydrate intake (de Castro, 1995b). Another significant source of individual differences is ageing. Above 50 years of age there appears to be a significant decrease in intake that results from a decrease in fat and protein intake (de Castro, 1993d). As a result the proportion of carbohydrate in the diet markedly increases with age.

Macronutrient intake regulation

Meal-to-meal regulation

Meal-to-meal regulation involves adjustments of the amount ingested in meals, the meal size, and/or the time interval between meals. It has been demonstrated in free-feeding laboratory conditions for both laboratory animals (LeMagen & Tallon, 1966, 1968; de Castro, 1975) and for human subjects (Bernstein *et al.* 1981) that the meal size tends to predict the duration of the following interval. This finding suggests that regulation of intake occurs via adjustments to the interval until the next meal. However, for human subjects in the natural environment this relationship is not significant (de Castro & Kreitzman, 1985; de Castro *et al.* 1988b). On the other hand, there is a significant relationship between the duration of the interval before a meal and the size of the meal (de Castro & Kreitzman, 1985; de Castro *et al.* 1988b). The duration of the before-meal interval is related to the amounts of each of the macronutrients ingested. This relationship appears to be due to the environmental constraints of the natural environment that do not allow individuals the luxury of eating when they want, and can thus only adjust intake by altering how much they eat (Bernstein *et al.* 1981; de Castro, 1988b). This finding suggests that individuals in their natural environment adjust the amount eaten in a meal based on how long it has been since they last ate; i.e. they regulate by adjusting meal size to their deprivation level.

Over the interval between meals the stomach empties. It makes intuitive sense that the amount remaining in the stomach at the time of meal ingestion would have a negative effect on subsequent intake; with the more present, the smaller the amount ingested in the subsequent meal (de Castro & Kreitzman, 1985). This factor could be responsible for the relationship between the before-meal interval and the meal size. We have taken advantage of the fact that the stomach empties in a very regular and predictable fashion (Hopkins, 1966; Hunt & Knox, 1968; Hunt & Stubbs, 1975) to calculate how much should have emptied over the interval and, hence, how much should be remaining at the time of the meal. As expected, we found a significant negative correlation between the amount predicted to be in the stomach at the point of meal initiation, and the meal size (de Castro & Kreitzman, 1985; de Castro *et al.* 1986; de Castro, 1987b, 1988a). This negative correlation was found regardless of whether meal size and/or stomach content was expressed in terms of total food energy, carbohydrate, fat or protein intake. Hence, there was a thoroughly reasonable finding that, even for free-living human subjects, the more food

energy or macronutrients present in the stomach at the beginning of the meal, the less will be eaten at the meal.

The data suggest that protein in the stomach has a particularly potent restraining effect on intake. This effect can be seen with the slopes of the regression lines from the stomach content *v.* meal size analyses (Fig. 3). The amount of protein in the stomach has significantly ($P < 0.05$) larger negative slopes than those for the other macronutrients. Indeed, the average slope for protein stomach content is -1.92 kJ/kJ for the prediction of overall food energy intake in the meal. This value indicates that the size of the meal is reduced by almost 2 kJ for every kJ protein in the stomach at the beginning of the meal.

The larger the meal the more of each of the macronutrients tends to be eaten. As a result the intakes of the macronutrients are positively correlated. This relationship makes it impossible to discern the independent impact of each macronutrient. Fortunately, multiple linear regression analysis allows the discernment of the effect of each macronutrient while mathematically holding constant the effects of the other two macronutrients. Multiple regression was used to predict the meal size on the basis of the predicted before-meal stomach contents of the three macronutrients (Fig. 4). Once again, protein stands out. It has a large and significant ($P < 0.05$) restraining effect on subsequent intake, while fat and carbohydrate have either no significant impact or a slight positive relationship with intake. In addition, protein produced a significantly ($P < 0.05$) larger negative beta coefficient when predicting the meal size of the meal size, indicating that protein is particularly potent in suppressing subsequent protein intake. An interesting conclusion from these results is that the effectiveness of the before-meal stomach contents in suppressing subsequent intake is not due to either fat or carbohydrate, but rather it appears to be exclusively due to protein.

Genetic influences

The degree to which the intakes of specific nutrients are heritable indicates long-term regulatory influences. In order to take a look at this factor, diet diary data of the overall and separate meal intakes of nutrients of identical and fraternal twins were analysed (de Castro, 1993a,b,c, 1998a, 1999) with linear structural modelling heritability analysis techniques (Heath *et al.* 1989; Neale & Cardon, 1992). The models revealed that the amount of food energy ingested daily as well as its macronutrient, alcohol and water contents were significantly affected by inheritance (de Castro, 1993a). Indeed, 65 % of the variance in daily energy intake could be attributed to heredity. In addition, heredity affected the pattern of intake. The analysis suggested that 44 % of the variance in meal frequency and 65 % of the variance in average meal size were due to heredity (de Castro, 1993a). In addition, the effects of genes on intake appear to be independent of their effects on body size (de Castro, 1993b).

Daily intake is composed of macronutrient intakes. Hence, it is possible that the apparent heritability of macronutrient intakes is a secondary consequence of the

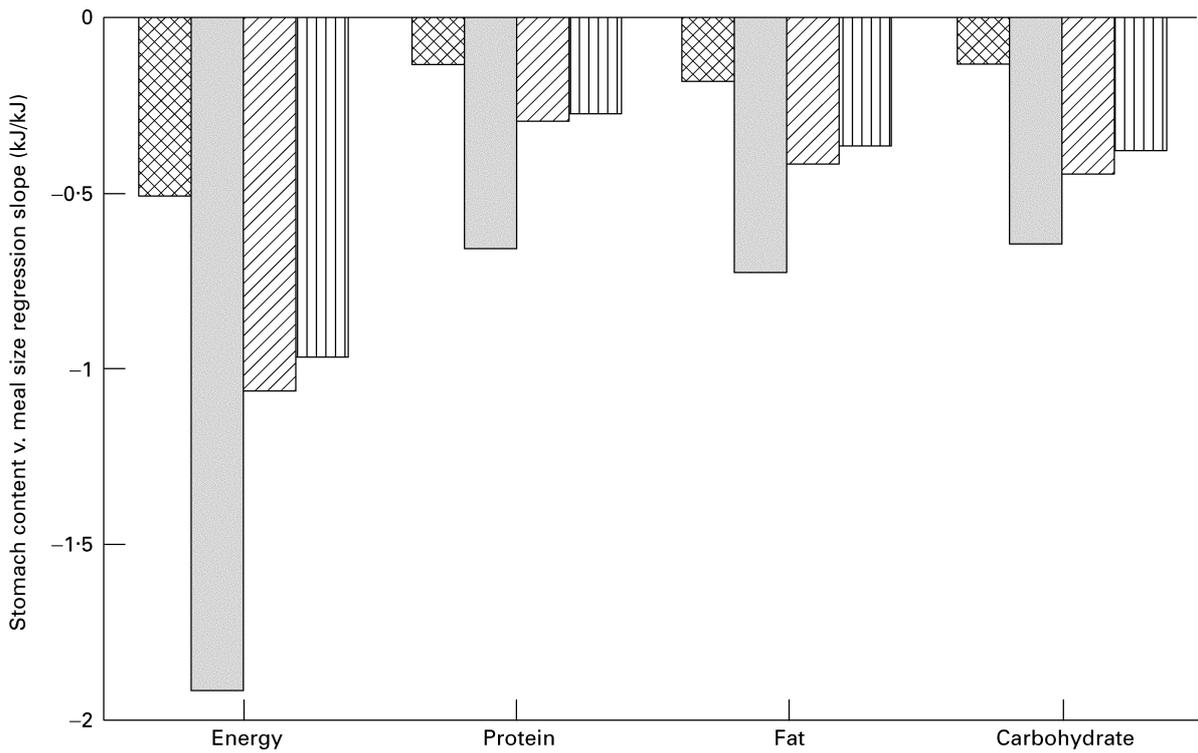


Fig. 3. Mean slopes of the regression lines relating the amounts ingested in the meals of total food energy, protein, fat or carbohydrate and the estimated before-meal stomach contents of total food energy (▨), protein (▤), fat (▥) and carbohydrate (▧).

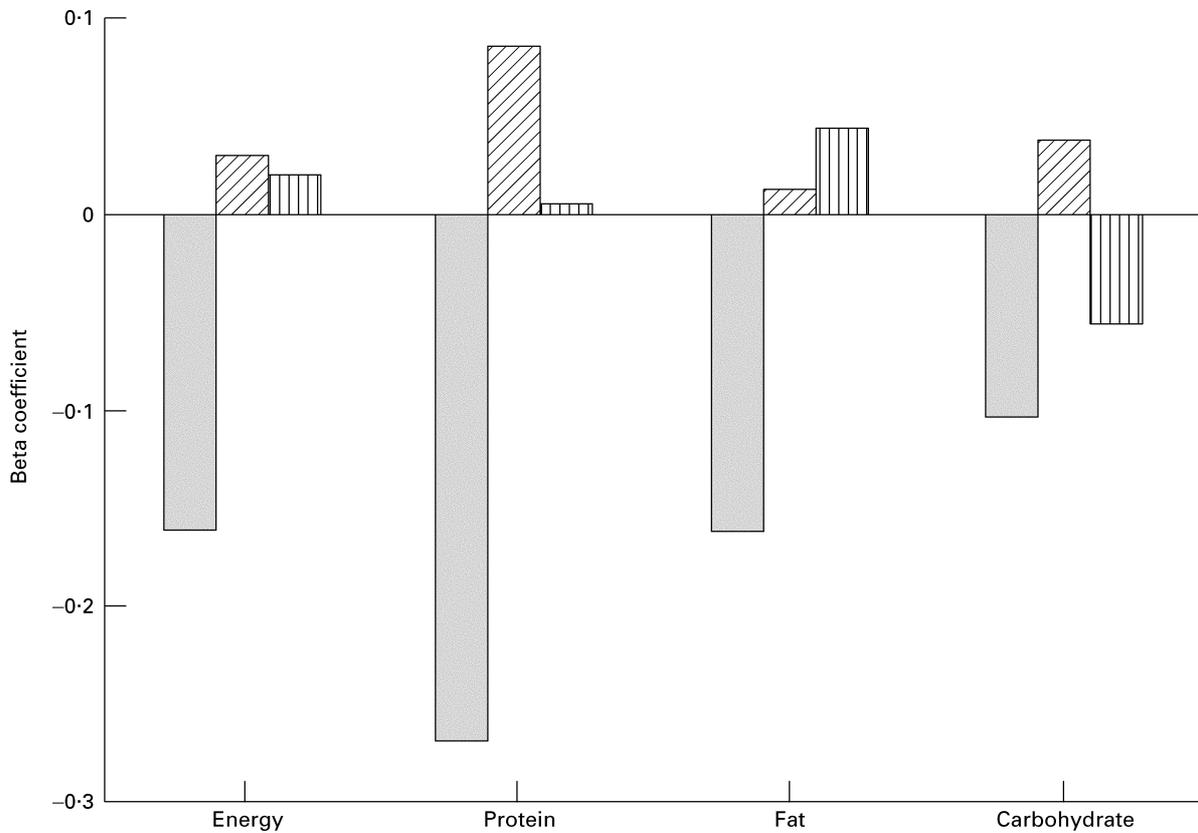


Fig. 4. Mean beta coefficients from four multiple linear regressions predicting the amounts ingested in the meals of total food energy, protein, fat or carbohydrate based on the independent variables of the estimated before-meal stomach contents of protein (▤), fat (▥) and carbohydrate (▧).

inheritance of daily food intake patterns. However, the heritability of macronutrient intake appears to some extent to be independent (de Castro, 1993b). A linear structural model applied to the twin data (Fig. 5) revealed that, taking overall intake into consideration, the genes still accounted for only 8, 10, and 7 % of the variance in the daily intake of carbohydrate, fat and protein respectively. The fact that there is still a residual effect of the genes on the daily intake of each of the macronutrients individually when their combined effects are removed is remarkable. Hence, there appear to be significant ($P < 0.05$) genetic influences on individual macronutrient intakes, independent of genetic effects on overall intake.

As reviewed previously, the intake of macronutrients is affected by the amounts of these macronutrients remaining in the stomach at the time that the meal is initiated. The genes appear to affect all aspects of this process. The twin data indicate that the heritability accounts for from 36 to 48 % of the variance in both the before- and after-meal stomach contents of macronutrients (de Castro, 1999). Hence, the genes influence the level of macronutrients that tend to be found in the stomach before and after meals. Responsiveness to this stomach filling can be measured by the regression assessing the relationship between the stomach contents and the size of the subsequent meal. Significant heritabilities were found for both the correlations and slopes. The clearest and strongest heritabilities were present for protein in the stomach, with the genes accounting for from 18 to 34 % of the variance. These results suggest that the genes may act to regulate the amounts of macronutrients ingested, not only directly, but also indirectly by affecting the amounts of macronutrients found in the stomach at the beginning of the meals and the individual's responsiveness to these stomach contents.

Day-to-day regulation

Intake varies considerably from day to day (Balogh *et al.* 1971; Morgan *et al.* 1987; Tarasuk & Beaton, 1991). To investigate whether daily intake is responsive to intake on previous days, autocorrelations were calculated between macronutrient intakes recorded in the diaries on one day and those occurring on subsequent days (de Castro, 1998b; Fig. 6). The autocorrelations that lagged by 2 d were significantly stronger ($P < 0.05$) than with other delays. Hence, it appears that negative feedback tends to restrain intake and that the effect is maximal 2 d later, continues on the third day, but disappears by the fourth day. In addition, there appear to be macronutrient-specific effects. Carbohydrate intake had significantly larger correlations ($P < 0.05$) with the amount of carbohydrate, fat intake had significantly larger correlations ($P < 0.05$) with the amount of fat, and protein intake had significantly larger correlations ($P < 0.05$) with the amount of protein, for intake occurring 1 or 2 d later, but not 3 or 4 d later. These results were also obtained (de Castro, 1998b) employing simplex autoregressive linear structural models (Boomsma *et al.* 1989; Neale & Cardon, 1992) that do not assume that the error terms are uncorrelated. Hence, there appears to be a macronutrient-specific delayed negative feedback on daily intake, with carbohydrate maximally affecting carbohydrate, fat affecting fat, and protein affecting protein 2 d after ingestion.

Discussion

The results of the studies reviewed indicate that the intake of macronutrients of normal free-living human subjects is affected by a wide variety of factors that operate both over the short and long term. Even with the wide range of inter-

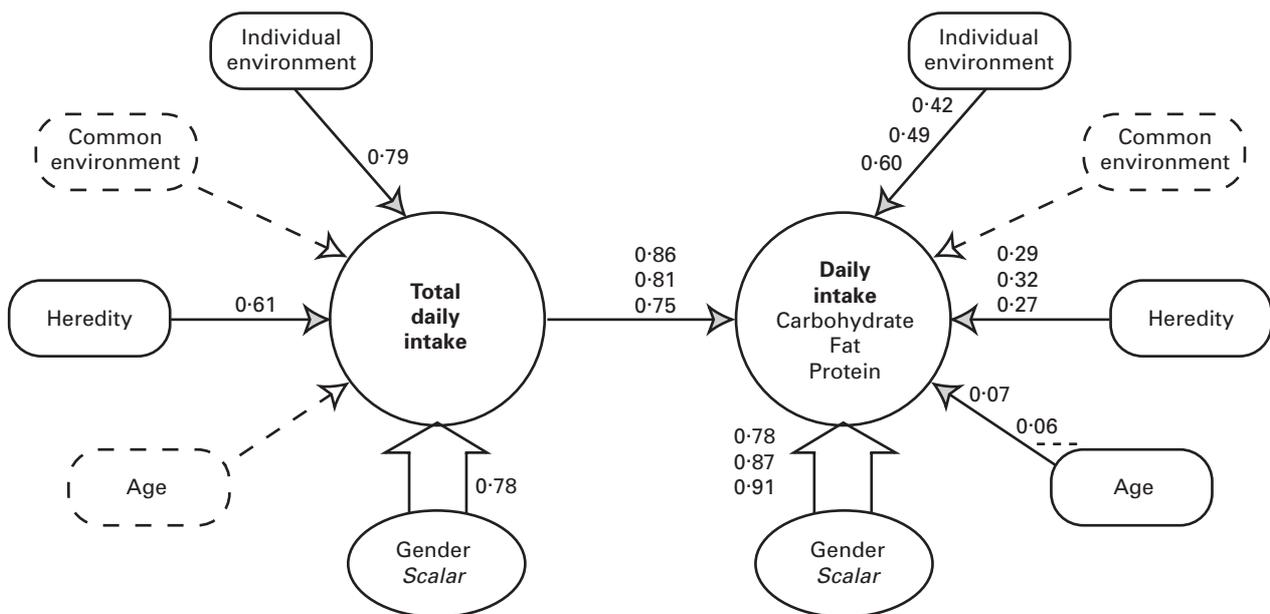


Fig. 5. Linear structural model showing the most parsimonious model fitting the twin data for total daily energy intakes and the daily intakes of carbohydrate, fat and protein (—). (---), Non-significant paths. Where three path coefficients are presented, coefficients represent the influence of the factor on carbohydrate, fat and protein intakes respectively. For all remaining variables, removing any one variable leads to a statistically significant reduction in the model's account of the observations. (---), Coefficient for protein was not significant.

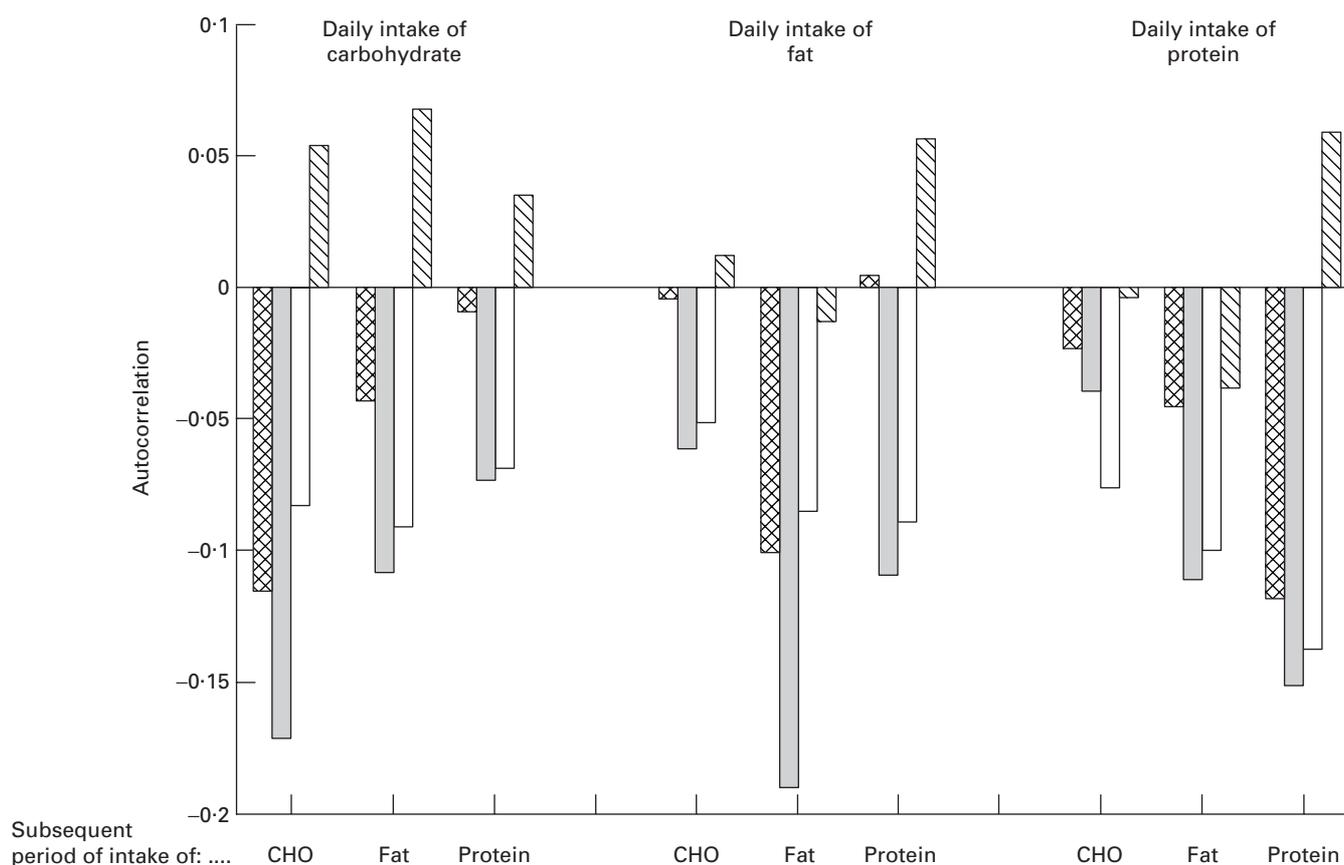


Fig. 6. Mean autocorrelation coefficients between daily intakes of carbohydrate, fat and protein and intake on subsequent days of carbohydrate, fat and protein. 1 (cross-hatch), 2 (solid grey), 3 (white), 4 (diagonal lines) are the correlations calculated between the amount ingested on one day and that on the next day, and 2, 3 and 4 d later respectively. (From de Castro, 1998b.)

and intra-individual factors there does appear to be a common trend. In particular, increased energy intake, almost regardless of cause, involves an increase in all macronutrients, but more so with fat and protein than carbohydrate. This trend results in an increase in the proportions of fat and protein ingested in the meal and a decrease in the proportion of carbohydrate. This situation occurred with increased energy intake due to: environmental factors such as social facilitation and the time of day, week, or lunar phase; subjective factors such as hunger and elation; individual difference factors such as obesity, restraint and ageing. The only exception was the case of the increase in energy intake occurring in the autumn which showed a proportionate increase in carbohydrate intake. Hence, in general, factors that promote intake tend to promote fat and protein intake to a greater extent than carbohydrate intake.

These influences do not appear to operate in isolation. The results suggest that there are significant regulatory influences that operate, and that these may compensate for over- or under-ingestion of the macronutrients. Over the short term, intake appears to be adjusted via a negative feedback process primarily involving protein. In particular, the amount of protein remaining in the stomach at the beginning of a meal appears to suppress the amount of all nutrients ingested. Protein appears to be suppressed to a greater extent than carbohydrate or fat, but nonetheless they all appear to

be negatively affected by the amount of protein in the stomach remaining from previous meals. This process appears to be affected by inheritance, with both the amount that an individual normally has in the stomach at the beginning of a meal and the degree of response to this stomach content being affected by the genes. In this way, short-term macronutrient intake can be regulated and the genes can affect it by influencing the stomach content negative feedback loop.

The negative feedback from stomach protein may be fairly non-selective, because it is difficult for the system to detect and meter the amounts of different nutrients present in a mixed heterogeneous meal. In order to adjust the intake of the macronutrients, the amounts ingested have to be measured. This measurement is very difficult to do based on the stimuli from the oral cavity. It is simpler for the system to monitor the nutrient quantities as they are digested and absorbed, and use these measurements to selectively affect the next meal. Hence, if protein is over-ingested there will be more protein in the stomach at the time of the next meal, and this factor will suppress intake at that meal. This process should result in less protein being ingested. However, if it does not, then the ingested protein will suppress intake at the next meal.

This short-term negative feedback mechanism only accounts for a small proportion of the variance in meal

intake and does not account for the large variation in day-to-day intake (Balogh *et al.* 1971; Morgan *et al.* 1987; Tarasuk & Beaton, 1991). This day-to-day variation in macronutrient intake appears to be affected by a different mechanism that involves a delayed negative feedback acting over a period of days, peaking at a 2 d delay. The mechanism appears to have a great deal of macronutrient specificity, such that intake of protein has a maximum suppressive effect on the intake of protein 2 d later, while carbohydrate suppresses carbohydrate and fat suppresses fat, also with a 2 d delay.

The mechanism by which macronutrients specifically affect this delayed negative feedback is unknown and may not be unitary. A period of 2 d is a very long time relative to the life of most gastrointestinal, plasma and hepatic factors, making these unlikely intermediaries. It is possible that feedback from adipose tissue may be involved in fat regulation. However, for carbohydrate and protein storage, half-lives are far too short and the turnover too high to allow for a 2 d feedback signal.

It should be noted that in general the sizes of the effect are small, which is not surprising given that in natural environments there are complex arrays of stimuli that affect the individual and create variance in behaviour. That single variables, e.g. negative feedback, only account for a small proportion of the variance may simply be a reflection of the fact that there are large numbers of variables operative in these environments. However, the data on inheritance suggest that the physiology, as determined by the genes, may have influences on a wide range of processes. The data imply that the genes may influence behavioural tendencies and preferences, and the individual's responsiveness to environmental factors. Thus, the factors that appear to be noise themselves may be affected by inherited physiological processes. Each process may only account for a small proportion of the variance, but the sum total of all the processes could account for most of the variance and result in the regulation of nutrient intakes.

Another important aspect of these inherited mechanisms is that they are persistent. Non-regulatory short-term influences do not persist. Over time they average and cancel out the effects of one another, and as a result have no net effect on intake. On the other hand, the effects of the genes persist, setting a bias which continues to influence intake and produces a cumulative net alteration of intake. In effect, over time the integral of the effects of the short-term environmental factors is zero, while the integral for the genetic effects, which individually produce only small negative feedback effects, becomes substantial. It has been suggested that over long periods of time these multiple persistent processes result in the regulation of the intake of the macronutrients.

Acknowledgements

Supported in part by Grant R01-DK39881 from the National Institute of Diabetes and Digestive and Kidney Diseases and from grants from the Georgia State University Research Enhancement Program.

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