Relation of Body Energetic Status to Dietary Self-Selection in Sprague-Dawley Rats

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Summary Self-selection from carbohydrate, protein and fat sources including essential micronutrients was studied in male Sprague-Dawley rats that were 4 weeks of age at the beginning of the experiment. During the experimental period of 14 days, the intake of carbohydrate and fat was quite constant, whereas that of protein increased gradually. The mean intake of carbohydrate, protein, and fat was 31.1 ± 3.5%, 56.1 ± 4.6%, and 12.8 ± 2.8% of the total energy intake, respectively. Animals fed on a mixed diet consisting of high sucrose, consumed 65.1% of their daily energy as carbohydrate, 17.6% as protein, and 17.3% as fat. Total energy intake and body weight gain were not significantly different between the rats on self-selection and those fed on the mixed diet. These results indicate that young rats on dietary self-selection were able to gain body weight comparable to that of rats fed on the mixed diet. Body energetic status affected self-selection patterns. In rats fasted for 5 days or fed on a protein-free diet for 21 days, fat intake increased, but protein intake decreased. On the other hand, fat intake decreased in animals given a sucrose diet higher in energy content than the stock diet; these animals exhibited increased accumulation of body energy. These results indicate that dietary self-selection is closely related to nutritional and physiological body requirements.

Key Words body energetic status, self-selection, dietary fat

No single natural food source contains adequate amounts of all the dietary elements necessary to sustain growth in omnivorous animals. Thus, it is necessary for these animals to regulate the intake of individual food components to maintain an adequate nutritional status (1); they must not only consume sufficient amounts of food to meet energy needs, but also select a balanced diet from foods varying widely in nutritional value. Dietary self-selection experiments designed to elucidate
the mechanisms by which such regulation is achieved have often given variable results (2–6).

Self-selection patterns of rats have been used to identify factors contributing to energy regulation and growth. Such patterns are affected by physiological and environmental variables such as pregnancy (7, 8), lactation (8), exposure to cold (9), responses to various drugs (10–13), and neuronal damage (14–16).

However, there are no fundamental data for these kinds of experiments in the young rat. Therefore, in this study, we begin with a description of the characteristics of self-selection of our diets by rats. We then investigate the changes of dietary choice in animals subjected to disturbances which modify energy intake. Thus, we observed three new facts: the achievement of full growth also in young rats; a decrease in fat intake after an increase in body energy; and an increase in fat intake after a long period of protein deficiency.

METHODS

Animals and diets. Male Sprague-Dawley rats (Jcl: SD, Clea Japan, Inc., Tokyo) were used. They were housed individually in wire-mesh hanging cages in a room controlled for temperature (23 ± 1°C), humidity (55 ± 5%), and light (08:00–20:00 h). They were kept under various nutritional conditions such as total starvation, a stock diet (CE-2, 352 kcal/100 g, Clea Japan, Inc., Tokyo), a high-sucrose diet, or a protein-free diet, and then subjected to dietary self-selection. The

Table 1. Composition of dietary sources and experimental diet (%).

| Ingredients                        | Carbohydrate source | Protein source | Fat source | High-sucrose diet | Protein-free diet |
|------------------------------------|---------------------|----------------|------------|------------------|------------------|
| Sucrose                            | 93.9                | —              | —          | 67.6             | 85.9             |
| Casein¹                            | —                   | 92.4           | —          | 18.0             | —                |
| DL-Methionine                      | —                   | 1.5            | —          | 0.3              | —                |
| Hydrogenated coconut oil²          | —                   | —              | 70.15      | —                | —                |
| Cottonseed oil                     | —                   | —              | —          | 16.11            | 8.0              |
| Vitamin mixture³                   | 0.5                 | 0.5            | 1.13       | 0.5              | 0.5              |
| Choline chloride                   | 0.1                 | 0.1            | 0.23       | 0.1              | 0.1              |
| Cellulose powder                   | 1.5                 | 1.5            | 3.38       | 1.5              | 1.5              |
| Salt mixture⁴                      | 4.0                 | 4.0            | 9.00       | 4.0              | 4.0              |
| Energy (kcal/100 g)⁵               | 375.6               | 357.2          | 446.30     | 412.0            | 415.6            |

¹ Casein used contained 95.0% protein (N × 6.25) (Wako Pure Chemical Industries, Ltd., Osaka). ² Econa® (Kao Food Co., Ltd., Tokyo). ³ Matsuo and Suzuoki (26). ⁴ Hegsted et al. (27). ⁵ The energy value was calculated applying the coefficients 4, 9 and 4 kcal for protein, fat and carbohydrate, respectively.
composition of the three dietary sources and of the experimental diets is presented in Table 1. All diets were held in glass food-containers equipped with metal discs (CL-0920, Clea Japan, Inc., Tokyo). Spillage was negligible for powdered diets such as carbohydrate and protein sources, but was occasionally observed for fat sources in greasy form. Therefore, fat intake was corrected for spillage. On the self-selection regime, three food containers, each filled with a different nutrient, were given to each animal. The containers were placed at random in the cages and could be moved around by the rats, thereby precluding place conditioning. Every day at 09:00 h, each rat was weighed, and its food containers were weighed and refilled. Food and water were available at all times unless otherwise stated.

**Body weight and energy intake of rats on dietary self-selection.** Four-week-old rats were given a high sucrose diet or three dietary sources of protein, carbohydrate, and fat for 14 days.

**Effects of antecedent nutritional status on dietary self-selection.** Dietary self-selection patterns were examined for 3 days in 7-week-old rats given the stock diet, a high-sucrose diet, or protein-free diet for 21 days, and in 8-week-old rats given the stock diet or fasted for 5 days.

**Analyses of carcass composition.** Carcass analyses were done on 7-week-old rats fed on the stock diet or high-sucrose diet for 21 days. These rats were killed by decapitation, and the blood and contents of gastrointestinal tracts were removed. The carcasses were weighed and homogenized with a motor-driven mincer (Type KU-1, Erweka Apparatebau-GmbH, Offenbach, Main). An aliquot (about 5 g) of the homogenate was dried to constant weight at 80°C. The dried carcasses were subjected to lipid extraction with chloroform–methanol (2:1) (17), and total lipids were measured gravimetrically. An aliquot of dried, lipid-extracted carcasses was subjected to total nitrogen analysis by the Kjeldahl procedure (18). Protein content was expressed by total nitrogen × 6.25.

**Statistical analysis.** The data reported are the means with their standard errors, and statistical significance was determined between means by use of Student’s unpaired t-test (19).

**RESULTS**

The body weight of rats on the self-selection regime increased comparable to that of rats fed on the mixed high-sucrose diet (Fig. 1); body weight at the termination of the former regime was 179 ± 3 g for the self-selection group and 188 ± 4 g for the mixed diet group. These values were not significantly different. Although daily energy intake tended to be lower in the self-selection group than in the mixed diet group, the total energy intake for 14 days was not significantly different: 864 ± 27 kcal for the self-selection and 922 ± 29 kcal for the mixed diet group (Fig. 2). These results indicated that young animals on the self-selection regime were able to select macronutrients to maintain growth comparable to that for those rats on the mixed diet.

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Fig. 1. Body weight of rats given a high-sucrose diet (●) or self-selection regime (○). Means ± SEM or means for 8 rats.

Fig. 2. Energy intake of rats given a high-sucrose diet (●) or self-selection regime (○), and energy intake from protein (□), carbohydrate (△) and fat (×) in rats maintained on the self-selection regime. Means ± SEM or means for 8 rats.

In the self-selection group, carbohydrate and fat intake remained nearly constant, but protein intake increased continually during the experimental period (Fig. 2). The energy intake from protein was 36.7 ± 4.7% on day 1, but gradually
increased to reach a maximum of $66.6 \pm 4.2\%$ on day 14. The animals chose a daily average of $56.1 \pm 4.6\%$ of their energy as protein, $31.1 \pm 3.5\%$ as carbohydrate and $12.8 \pm 2.8\%$ as fat. Animals fed on the high-sucrose diet obtained $17.6\%$ of their daily energy as protein, $65.1\%$ as carbohydrate, and $17.3\%$ as fat.

Dietary self-selection patterns were similar among the rats prefed the stock diet regardless of age (Table 2, A, B, and E). In animals given the high-sucrose diet, energy intake was similar to, but fat intake was less than, the corresponding values for those given the stock diet (Table 2, B and C). In rats prefed the protein-free diet for 21 days, energy intake gradually increased from day 1 to 3 of the self-selection regime (Table 2, D). Some marked differences in the distribution of energy intake were evident between rats fed on the high-sucrose diet and those fed on the protein-free diet (Table 2, C and D). The main difference was the inverse change in fat and protein intake: in the protein-free diet group, fat intake increased, whereas protein intake decreased. Carbohydrate intake was unaffected. In fasted rats, energy intake gradually increased from day 1 to 3 (Table 2, F). These rats preferentially consumed fat, but decreased protein intake especially on day 1.

There was no difference in body weight between rats fed on the stock diet and those fed on the high-sucrose diet (Table 3). However, feeding the high-sucrose diet resulted in an increase of fat deposition and a decrease of moisture (Table 3). Carcass protein tended to increase in rats fed on the high-sucrose diet. Therefore, body energy content was $25\%$ higher in the high-sucrose diet group than in the stock diet group.

**DISCUSSION**

The results of the present experiments demonstrate that young Sprague-Dawley rats on dietary self-selection are able to gain body weight comparable to the case with rats fed on a mixed diet. Energy intake was similar for the two groups, but its distribution was considerably different. Rats fed on the mixed diet consumed $65.1\%$, $17.6\%$ and $17.3\%$ from carbohydrate, protein and fat, respectively. On the other hand, in rats on the self-selection regime, energy intake from protein was $36.7 \pm 4.7\%$ on day 1, and gradually increased to reach a maximum of $66.6 \pm 4.2\%$ on day 14; these values are much higher than those reported by other investigators (3–6, 14, 20). Scott and Quint reported that rats kept under self-selection could be separated into two groups on the basis of their appetite for casein (21), which is reported to be relatively unpalatable to rats (1, 7, 15). The failure of animals to maintain body weight on a self-selection regime most frequently results from an inadequate intake of casein (1, 4, 7, 15). In the present study, however, animals preferentially consumed casein on the self-selection regime. Although differences between the results of other experiments (1, 7, 15) and those of the present ones are not clear, some factors such as diet palatability, the number of choices available to the animals, the strain or the age of the animals used, and other unknown components of the experimental environment may cause these differences.
Table 2. Dietary self-selection of rats kept under various nutritional conditions. \(^1\)

| Conditions before selection | N | Age at start of selection (weeks) | Days after selection (days) | Body weight (g) | Energy intake (kcal/day) | Energy intake from Carbohydrate (%) | Protein (%) | Fat (%) |
|-----------------------------|---|----------------------------------|-----------------------------|----------------|-------------------------|-----------------------------------|-------------|---------|
| A. Stock diet               | 8 | 4                                | 0                           | 85 ± 1         | 46.5 ± 4.8* 34.3 ± 4.7* 19.2 ± 3.7* |                                    |             |         |
|                             |   |                                  | 1                           | 86 ± 1         | 41.1 ± 2.2* 39.0 ± 4.7* 17.6 ± 2.9* |                                    |             |         |
|                             |   |                                  | 2                           | 91 ± 1         | 43.2 ± 1.5* 41.1 ± 4.1* 12.3 ± 1.2* |                                    |             |         |
|                             |   |                                  | 3                           | 97 ± 1         | 53.4 ± 2.7* 41.1 ± 3.7* 18.6 ± 4.0* |                                    |             |         |
| B. Stock diet               | 6 | 7                                | 0                           | 236 ± 7        | 45.7 ± 4.6* 37.2 ± 3.8* 17.1 ± 3.6* |                                    |             |         |
|                             |   |                                  | 1                           | 242 ± 4        | 82.1 ± 4.6* 40.3 ± 3.4* 18.6 ± 4.0* |                                    |             |         |
|                             |   |                                  | 2                           | 249 ± 5        | 83.9 ± 4.7* 41.1 ± 3.7* 18.6 ± 4.0* |                                    |             |         |
|                             |   |                                  | 3                           | 256 ± 6        | 76.4 ± 3.3* 39.3 ± 4.3* 44.2 ± 3.5* 16.4 ± 3.2* |                                    |             |         |
| C. High-sucrose diet        | 6 | 7                                | 0                           | 239 ± 9        | 50.6 ± 8.1* 37.7 ± 8.3* 11.7 ± 1.8* |                                    |             |         |
|                             |   |                                  | 1                           | 242 ± 6        | 50.8 ± 4.7* 42.3 ± 4.1* 6.9 ± 1.8* |                                    |             |         |
|                             |   |                                  | 2                           | 248 ± 7        | 83.9 ± 4.7* 41.1 ± 3.7* 18.6 ± 4.0* |                                    |             |         |
|                             |   |                                  | 3                           | 252 ± 4        | 70.1 ± 1.9* 41.9 ± 5.6* 50.5 ± 6.2* 7.6 ± 1.3* |                                    |             |         |
| D. Protein-free diet        | 6 | 7                                | 0                           | 67 ± 2         | 44.0 ± 5.8* 11.3 ± 4.8* 44.7 ± 7.1* |                                    |             |         |
|                             |   |                                  | 1                           | 72 ± 5         | 41.3 ± 5.3* 48.2 ± 6.1* 20.3 ± 3.4* 31.5 ± 6.3* |                                    |             |         |
|                             |   |                                  | 2                           | 77 ± 6         | 83.9 ± 4.7* 41.1 ± 3.7* 18.6 ± 4.0* |                                    |             |         |
|                             |   |                                  | 3                           | 85 ± 5         | 47.0 ± 2.7* 53.6 ± 3.3* 17.0 ± 2.5* 29.4 ± 4.0* |                                    |             |         |
| E. Stock diet               | 6 | 8                                | 0                           | 301 ± 8        | 47.1 ± 2.8* 36.9 ± 3.3* 16.0 ± 3.8* |                                    |             |         |
|                             |   |                                  | 1                           | 295 ± 7        | 98.0 ± 4.9* 38.8 ± 4.2* 44.8 ± 3.6* 16.4 ± 4.7* |                                    |             |         |
|                             |   |                                  | 2                           | 304 ± 7        | 98.0 ± 4.9* 38.8 ± 4.2* 44.8 ± 3.6* 16.4 ± 4.7* |                                    |             |         |
|                             |   |                                  | 3                           | 307 ± 8        | 88.0 ± 3.6* 40.6 ± 6.4* 44.4 ± 3.3* 15.0 ± 4.6* |                                    |             |         |
| F. Fasted                  | 6 | 8                                | 0                           | 189 ± 5        | 67.8 ± 7.4* 47.9 ± 3.1* 6.5 ± 2.9* 45.6 ± 5.2* |                                    |             |         |
|                             |   |                                  | 1                           | 203 ± 7        | 96.1 ± 5.9b 33.9 ± 2.6b 27.5 ± 3.5b 38.6 ± 5.0b |                                    |             |         |
|                             |   |                                  | 2                           | 219 ± 8        | 96.1 ± 5.9b 33.9 ± 2.6b 27.5 ± 3.5b 38.6 ± 5.0b |                                    |             |         |
|                             |   |                                  | 3                           | 238 ± 9        | 123.9 ± 8.8c 30.3 ± 2.4b 29.1 ± 5.1b 40.6 ± 6.7a |                                    |             |         |

Statistical comparisons:

| A vs. B | 1 | p | NS | NS | NS | NS |
|         |   |   |    |    |    |    |
| A vs. C | 1 | <0.001 | NS | NS | NS | NS |
|         |   | <0.001 | NS | NS | NS | NS |
| A vs. D | 1 | <0.001 | NS | <0.01 | <0.02 | NS |
|         | 2 | NS | NS | <0.01 | <0.02 | NS |
| A vs. E | 1 | <0.001 | NS | NS | NS | NS |
|         | 2 | <0.001 | NS | NS | NS | NS |
|         | 3 | <0.001 | NS | NS | NS | NS |

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Table 2. (continued)

| Conditions before selection | N | Age at start of selection (weeks) | Days after selection (days) | Body weight (g) | Energy intake (kcal/day) | Energy intake from Carbohydrate | Protein (%) | Fat |
|-----------------------------|---|----------------------------------|-----------------------------|-----------------|-------------------------|---------------------------------|-------------|-----|
| A vs. F                     | 1 | <0.01                            | NS                          | <0.001          | <0.01                   | <0.01                           |             |     |
|                             | 2 | <0.001                           | NS                          | <0.001          | <0.02                   | <0.01                           |             |     |
|                             | 3 | <0.001                           | NS                          | <0.05           | <0.01                   | <0.01                           |             |     |
| B vs. C                     | 1 | NS                               | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 2 | NS                               | NS                          | NS              | <0.05                   | NS                              |             |     |
|                             | 3 | NS                               | NS                          | NS              | NS                      | NS                              |             |     |
| B vs. D                     | 1 | <0.001                           | NS                          | <0.01           | <0.01                   | NS                              |             |     |
|                             | 2 | <0.001                           | NS                          | <0.01           | NS                      | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.05           | <0.01                   | NS                              |             |     |
| B vs. E                     | 1 | <0.02                            | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 2 | <0.05                            | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 3 | <0.05                            | NS                          | NS              | NS                      | NS                              |             |     |
| B vs. F                     | 1 | NS                               | NS                          | <0.001          | <0.01                   | NS                              |             |     |
|                             | 2 | NS                               | NS                          | <0.05           | <0.01                   | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.05           | <0.01                   | NS                              |             |     |
| C vs. D                     | 1 | <0.001                           | NS                          | <0.05           | <0.01                   | NS                              |             |     |
|                             | 2 | <0.001                           | NS                          | <0.01           | <0.01                   | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.01           | <0.01                   | NS                              |             |     |
| C vs. E                     | 1 | <0.02                            | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 2 | NS                               | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 3 | NS                               | NS                          | NS              | NS                      | NS                              |             |     |
| C vs. F                     | 1 | NS                               | NS                          | <0.01           | <0.001                  | NS                              |             |     |
|                             | 2 | NS                               | NS                          | <0.05           | <0.001                  | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.05           | <0.01                   | NS                              |             |     |
| D vs. E                     | 1 | <0.001                           | NS                          | <0.01           | <0.02                   | NS                              |             |     |
|                             | 2 | <0.001                           | NS                          | <0.001          | NS                      | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.001          | NS                      | NS                              |             |     |
| D vs. F                     | 1 | <0.02                            | NS                          | NS              | <0.02                   | NS                              |             |     |
|                             | 2 | <0.001                           | NS                          | NS              | NS                      | NS                              |             |     |
|                             | 3 | <0.001                           | NS                          | <0.001          | NS                      | NS                              |             |     |
| E vs. F                     | 1 | <0.02                            | NS                          | <0.001          | <0.01                   | NS                              |             |     |
|                             | 2 | NS                               | NS                          | <0.01           | <0.02                   | NS                              |             |     |
|                             | 3 | <0.01                            | NS                          | <0.05           | <0.05                   | NS                              |             |     |

1 Data are means ± SEM. Values not followed by the same letter superscript are significantly different (p < 0.05); the comparisons are vertical and were made within diets between days. NS, not significant.

The present study demonstrates that dietary self-selection is governed by the nutritional state of rats. Animals given the protein-free diet for 21 days were anorectic and lost body weight. On dietary self-selection, these rats did not show an...
Table 3. Effect of a high-sucrose diet on body composition. ¹

|                          | Stock diet       | High-sucrose diet |
|--------------------------|------------------|-------------------|
| Number of animals        | 6                | 10                |
| Body weight (g)          | 242 ± 4.0        | 240 ± 3.7         |
| Carcass                  |                  |                   |
| Weight (g)               | 225 ± 2.1        | 227 ± 1.8         |
| Moisture (g)             | 156.7 ± 3.9      | 145.6 ± 2.3⁴      |
| Protein (g)              | 41.8 ± 1.3       | 44.5 ± 0.7        |
| Fat (g)                  | 15.7 ± 1.1       | 23.1 ± 1.2⁵       |
| Energy (kcal)            | 309 ± 6.2        | 386 ± 8.1⁶        |

¹ Data are means ± SEM. The energy value was calculated applying the coefficients 4 and 9 kcal for protein and fat, respectively. Significantly different from stock diet (*p < 0.05, ⁵p < 0.001).

immediate compensatory increase of protein intake. This result is in marked contrast to that of Piquard et al. (5), who observed that protein intake was increased two-fold and compensated exactly for by the protein lack. This difference has some important implications for dietary selection. We have assumed that this difference can be related to the difference in age of animals used and the duration of protein deprivation. Piquard et al. (5) used 16-week-old rats and a 6-day period of protein deprivation, and energy intake of the animals was unchanged during this period. On the other hand, we used younger animals and a longer period of protein deficiency, and our animals seemed to suffer both protein and energy deficiency. Therefore, our results that animals have a tendency to choose fat over protein for recovery from energetic and protein deficiency, suggest that the regulation of energy intake predominates over that of protein intake.

The animals failed to overeat on the first day of dietary self-selection after a 5-day fast, in the present study. This may result from the lack of ingestional experience during fasting and also the gastric and intestinal changes caused by a lack of dietary bulk. An energy deficit, produced by fasting, was compensated by an increase in fat intake; fasted rats eat more fat in order to take in as much energy as possible in a small volume of food. This increased fat intake was also observed by other investigators (4, 5, 14) who used different sources of fat. These facts, therefore, suggest that increased fat intake could be related to changes in metabolic status during and after fasting.

In the present study, the energy surfeit was compensated for by a decrease in fat intake. Fat may be involved in the long-term regulation of food intake (22). Various investigators have noted a relation between body weight and fat intake, and in particular, that an increased intake is related to a decrease in body weight (4, 5, 23). Da Costa and Clayton (24) observed that in rats undernourished for 90 days, the recovery of lost body weight was possible only with a high-fat diet. Likewise stress,
resulting in a slight decrease in body weight, was accompanied by an increase in fat intake (25). Similar observations emerge from the data of Scott et al. (7). Thus, these results seem to argue in favor of the involvement of fat intake in food intake regulation. The present results, in conjunction with data from experiments on dietary selection (6, 11, 13), provide information on both the quantitative and qualitative aspects of feeding behavior, and stress the importance of this approach in investigations of feeding regulation.

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