

Mechanisms of diet selection: the translation of needs into behaviour

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DEFINING THE PROBLEM OF DIET SELECTION

As a starting point for investigating the *mechanisms* of diet selection it is worth considering the *function* of diet selection. First, it is clear that the animal must select from the available foods a diet which can satisfy its nutritional requirements. Second, in doing this it must avoid ingesting harmful substances. Third, it must exploit resources efficiently: for many animals food supplies are distributed unevenly in the environment, they may vary seasonally and the acquisition of food competes with other essential activities. Therefore, adaptive diet selection will reflect the structure of the animal's habitat. Indeed, animals appear to be very efficient in their foraging strategies, for example, trading off the quality of a resource against the cost of its procurement. This will not be discussed in detail here, but it is important to note that mechanistic hypotheses should be consistent with this ecological perspective. Collier (1986) argues that the animal is able to optimize its exploitation of resources because the physiological system can buffer variability in food intake (e.g. by mouth pouches, the crop, the stomach, fat storage, interchangeability of metabolic fuels, etc.). Such a conceptualization has a number of important implications. For example, it makes untenable the view that the goal of food intake is the maintenance of body fat stores (this does not deny that the level of body fat feeds back to influence intake, but it does suggest a wide tolerance in the level of body fat). At the same time there is little doubt that physiological changes can have profound effects on food preference. The powerful craving for carbohydrates characterized as 'hunger riot' following large doses of insulin, and the potent urge for salt and consumption of salty foods as a consequence of adrenocortical insufficiency provide two examples. However, while these instances serve to verify the influence of extreme physiological events, the arguments discussed previously suggest that under many circumstances relatively minor physiological perturbations may have no detectable effects on diet selection.

It is also important to note that the problems of satisfying nutritional requirements differ enormously according to the natural history of the species. For carnivores, detecting and capturing prey usually presents the primary challenge, whereas herbivores may have to graze for long periods (while avoiding being eaten themselves) in order to consume sufficient of what is relatively-poor-quality food. Omnivores are faced with a wider range of potential foods and accordingly their diet selection may depend more on learned influences (Rozin, 1976). Some of the mechanisms which operate to guide appropriate diet selection in omnivores such as rats and humans are reviewed later.

INNATE OROSENSORY PREFERENCES

There are certain taste preferences present at birth which can strongly bias diet selection. For example, the facial expressions of human newborns indicate acceptance and a

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positive hedonic response to sweet stimuli, while bitter stimuli evoke rejection coupled with negative expressions (Steiner, 1987). Such biases are considered to be adaptive in that bitter tastes tend to be correlated in nature with the presence of toxins, and sweet tastes will normally signal a ready source of food energy in the form of sugars (Rozin & Vollmecke, 1986). Even more significant, the universally enthusiastic response to sweetness may be an important factor contributing to the infant animal's acceptance of its mother's milk (D. A. Booth, personal communication). Recent results demonstrate that rodents also show a strong preference for starch-derived polysaccharides such as Polycose (partially hydrolysed maize starch with a sugar content of <100 mg/g), which humans find bland and report as unpleasant at high concentrations (Feigin *et al.* 1987). Rats, nonetheless, apparently taste Polycose as qualitatively different from sucrose and other sugars, and it has been suggested that they have two different taste (sub)systems for carbohydrates (Sclafani, 1987). This species difference is somewhat puzzling since starch-rich plants are staples in the human diet. A possible explanation lies in the fact that these staple foods, in contrast to sugar-rich fruits, tend not to be eaten raw but are usually cooked and flavoured with spices and sauces (Feigin *et al.* 1987). However, rather than making a polysaccharide taste system redundant, such practices may well have developed in response to the blandness of starchy foods.

In a similar way the presence of a salt taste receptor and preference for salt, together with the scarcity of this commodity in some habitats, can be understood in terms of the importance of maintaining sodium balance (Rozin, 1976). Also Deutsch *et al.* (1989) have demonstrated an unlearned preference for protein in protein-deprived rats, which appears to be based on olfactory cues. This is a particularly noteworthy finding in view of the controversy concerning the control of protein selection (see pp. 66–67). A further possibility is the existence of an innate preference for the texture of fat (Lucas & Sclafani, 1989). Notably taste qualities do not lose their identities in mixtures, therefore the presence of, for example, salt, sweet and bitter substances can be detected within complex foods (the analytic nature of taste; see Bartoshuk, 1989).

ENDOGENOUS REGULATORY SYSTEMS

If innate mechanisms exist to guide diet selection toward particular commodities such as salt, carbohydrates and protein then questions arise about the biochemical nature of those mechanisms. Logic demands that the need state (departure from some optimal value) must be detected and converted into a signal which drives behaviour and adjusts preference. This can be conceptualized as the translation of needs into behaviour and is the essence of motivational systems which give rise to adaptive behaviour. The detection system might involve adjustments in the sensitivity of specific receptors, for example salt receptors, glucoreceptors or amino acid receptors, or some other biochemical adjustment brought about by the lack of the required dietary component. The mechanism should be able to account for the adequate selection of the component under normal conditions and for the existence of 'craving' under conditions of severe deficit or imposed demand. The present discussion will concentrate on one proposed regulatory mechanism which has been the focus of scientific interest in recent years. This model, invokes changes in brain synaptic activity of the neurotransmitter serotonin as the key factor in macronutrient selection.

The hypothesis stipulates the existence of a bio-behavioural regulatory loop in which

the proportions of carbohydrate and protein in the diet lead to adjustments in the ratio of tryptophan to other (large neutral) amino acids in plasma. In turn this plasma ratio determines the amount of tryptophan entering the brain by competition for the transport system at the blood–brain barrier. The concentration of tryptophan, a precursor of serotonin, in the brain modulates the synthesis of serotonin and it is inferred that increased synthesis leads to enhanced release and, therefore, intensified receptor activation. Finally it is proposed that this activation of serotonin neurones leads to regulatory behaviour, namely the choice of appropriate amounts of protein and carbohydrate. (For physiological details of these relationships, see Wurtman *et al.* 1981.)

A recent review, however, concluded that there was only limited support for this hypothesis (Blundell *et al.* 1989). Different dietary intakes of macronutrients can alter the plasma ratio of tryptophan to other large neutral amino acids but the changes are small and fragile. While the presence of pure carbohydrate could, at least in principle, be detected by changes in brain serotonin synthesis, the experimental evidence suggests that many different mixtures of carbohydrate and protein all have the same effect. If brain tryptophan is to be the monitored variable, it seems that serotonin neurones could act as ratio sensors under certain special conditions. Accordingly the proposed mechanism might play some role in keeping food selection within nutritionally appropriate limits, for example, by preventing individuals endlessly consuming pure carbohydrate. It appears that the relationship between dietary macronutrients, brain serotonin and adaptive behaviour may be more complex than previously envisaged (Blundell & Hill, 1987). More generally, the previously-mentioned mechanism illustrates the components of a regulatory system: detection, translation and action.

LEARNED PREFERENCES AND AVERSIONS

It is well established that animals, especially omnivores, learn to avoid a food when consumption of that food is paired with illness, in particular nausea and gastrointestinal upset (Garcia *et al.* 1974). This learning can be very rapid, it can occur over long delays and is very persistent (i.e. it is hard to extinguish). At the same time it has been generally assumed that preferences could also be established on the basis of the positive ('nutritional') after-effects of food ingestion. However, clear evidence for learned preferences has been lacking until very recently. Using an 'electronic oesophagus' preparation Sclafani and his colleagues (e.g. Elizalde & Sclafani, 1990) were able to demonstrate strong conditioning of preferences for arbitrary flavours paired with intragastric Polycose infusions. The success of these elegant studies appears to derive from a number of important procedural features which, for example, reduced the possibility of aversive consequences arising from the intragastric infusions: Polycose has a low osmolarity compared with the infusates used in many of the earlier studies (e.g. glucose) and, furthermore, because the infusions are coupled to the animal's voluntary drinking they can be terminated before they become unduly discomforting. At present, it is not known what visceral stimuli (produced by the nutrients) underlie this flavour preference conditioning. However, it appears that both learned preferences and aversions are characterized by alterations in the hedonic evaluation of the food's taste, flavour, texture etc. (i.e. a change in palatability, Booth, 1979; Rogers, 1990). The advantage of an ability to modify a preference based on the benefit or otherwise derived

from consuming a food is obvious, and it is likely that such conditioning of palatability plays an important role in guiding diet selection.

SOCIAL TRANSMISSION OF FOOD PREFERENCES

Another powerful influence on food preferences is social contact. For example, young rats very readily acquire the same food preferences as adult members of their social group. This social transmission of food preferences can occur in a number of different ways, including through observation of adults at the feeding site, via chemical cues left at the feeding site and via flavour cues in maternal milk (Galef, 1982). Olfactory communication also appears to mediate the transmission of food preferences between adult rats (Galef & Wigmore, 1983; Strupp & Levitsky, 1984). For humans a wide range of social factors influences diet selection. Most obvious is the effect of culture and family custom which sets constraints on the type of foods to which an individual is exposed. Moreover, social interaction is in turn one of the factors influencing the development of preferences for those foods. The most rigorous studies of social learning in this context have been carried out by Birch (1986) and her colleagues who have demonstrated, for example, that the apparent social value of a food can affect preference. Thus, nursery school children showed stable increases in preferences for foods chosen by their peers. Preference was also enhanced if the food was given *as a reward*, whereas children 'bribed' (given an extrinsic reward) for eating a particular food showed a decline in preference for that food. There are practical implications of these last two results in that they contradict a practice often used by parents when feeding their young children: 'if you eat your greens you can have some ice cream'.

SHORT-TERM CHANGES IN FOOD PREFERENCE WITH EATING

Many studies have shown that consumption of a food can lead to a temporary shift in preference away from that food (e.g. Young, 1940). This, moreover, has been demonstrated where the choices were among foods that differed only in their flavour or odour (Morrison, 1974; Treit *et al.* 1983; Le Magnen, 1985). Such changes in relative preference for different orosensory stimuli would presumably extend the range of foods selected if the reversal of preference occurred before the end of the meal or if it lasted until the next meal (Holman, 1973; Rogers & Blundell, 1984). This could contribute to the selection of a nutritionally-adequate diet by increasing the variety of foods consumed. Furthermore, the sampling of a variety of different foods may lead to the acquisition of new preferences conditioned by the nutritional after-effects of food ingestion (see p. 67).

One explanation of the previously-mentioned findings is that there are sensory-specific decreases in the palatability of food during its consumption. This is supported by studies showing that human subjects report decreases in the 'pleasantness of the taste' of a food as it is eaten. For foods not eaten (in fact eaten in small amounts for rating purposes) there is a smaller decrease or no decrease in pleasantness depending on the similarity to the eaten food (Rolls *et al.* 1984). The decline in pleasantness is temporary, lasting perhaps a few hours (Hetherington *et al.* 1989). The interpretation of subjective ratings of pleasantness, however, presents a number of difficulties. Subjects' expectations will have a strong influence on their responses. Indeed, one view holds that reference to such

subjective experiences arises as a result of attempts to explain or justify personal actions (see Blundell, 1979). Although a person may report certain feelings or sensations this does not mean that these play a direct role in the causation of behaviour. Another explanation that could account for short-term fluctuations in food selection is simply that there is a general tendency to alternate choices. For example, rats placed in a 'T' maze alternate their choice of goal-arm in the absence of differential reinforcement ('spontaneous alternation behaviour', Richman *et al.* 1986). There is also good evidence that sensory contact with food has a stimulatory rather than inhibitory effect on eating (e.g. Rogers & Blundell, 1989). Therefore, alternation of food choices may be due to the re-stimulation of eating by sensory variety (and not to the avoidance of sensory-specific satiety) (for further discussion see Blundell & Rogers, 1991).

CONCLUSIONS

The previous discussion has reviewed some of the mechanisms that may operate to guide adaptive diet selection. Innate taste biases correlate with the need to ingest Na and energy sources and avoid poisons. Learning, however, also has a powerful influence on food preference. For example, palatability can be modified by the after-effects of food ingestion, leading to increases in acceptance of foods conferring nutritional benefit and avoidance of toxic substances. The existence of an innate mechanism regulating the selection of protein and carbohydrate within narrow limits has not been confirmed. Nonetheless, the proposed mechanism illustrates the features of such a regulatory system, namely the detection of need and its translation into a signal which drives behaviour and adjusts preference. Finally, it is also useful to view the problem of diet selection from an ecological perspective. Nutritional requirements have to be satisfied within the context of fluctuations in the availability of foods, and competition with other biologically essential activities. Accordingly certain physiological and behavioural adaptations may be best understood in terms of their contribution to the anticipation of needs and the optimal exploitation of resources.

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REFERENCES

- Bartoshuk, L. M. (1989). Taste: robust across the age span? *Annals of the New York Academy of Sciences* **561**, 65–75.
- Birch, L. L. (1986). The acquisition of food acceptance patterns in children. In *Eating Habits: Food, Physiology and Learned Behaviour*, pp. 107–130 [R. A. Boakes, D. A. Popperwell and M. J. Burton, editors]. Chichester: Wiley.
- Blundell, J. E. (1979). Hunger, appetite and satiety – constructs in search of identities. In *Nutrition and Lifestyles*, pp. 21–42 [M. Turner, editor]. London: Applied Science Publishing.
- Blundell, J. E. & Hill, A. J. (1987). Nutrition, serotonin and appetite: a case study in the evolution of a scientific idea. *Appetite* **8**, 183–194.
- Blundell, J. E., Hill, A. J. & Lawton, C. L. (1989). Neurochemical factors in normal and abnormal eating in humans. In *Handbook of the Psychophysiology of Human Eating*, pp. 85–112 [R. Shepherd, editor]. Chichester: Wiley.
- Blundell, J. E. & Rogers, P. J. (1991). Hunger, hedonics and the control of satiation and satiety. In *Chemical Sciences Vol. 4: Appetite and Nutrition* [M. A. Friedman and M. R. Kare, editors]. (In the Press.) New York: Marcel Dekker.

- Booth, D. A. (1979). Acquired behavior controlling energy intake and output. *The Psychiatric Clinics of North America* **1**, 545–579.
- Collier, G. (1986). The dialogue on strategy between the economist and the resident physiologist. *Appetite* **7**, 188–189.
- Deutsch, J. A., Moore, B. O. & Heinrichs, S. C. (1989). Unlearned specific appetite for protein. *Physiology and Behavior* **46**, 619–624.
- Elizalde, G. & Sclafani, A. (1990). Flavor preferences conditioned by intragastric infusions: a detailed analysis using an electronic esophagus preparation. *Physiology and Behavior* **47**, 63–67.
- Feigin, M. B., Sclafani, A. & Sunday, S. R. (1987). Species differences in polysaccharide and sugar taste preferences. *Neuroscience and Biobehavioral Reviews* **11**, 231–240.
- Galef, B. (1982). Studies in social learning in Norway rats: a brief review. *Developmental Psychobiology* **15**, 279–295.
- Galef, B. & Wigmore, S. W. (1983). Transfer of information concerning distant diets: a laboratory investigation of the “information centre” hypothesis. *Animal Behaviour* **31**, 748–758.
- Garcia, J., Hankins, W. G. & Rusiniak, K. W. (1974). Behavioural regulation of the milieu interne in man and rat. *Science* **185**, 824–831.
- Hetherington, M., Rolls, B. J. & Burley, V. J. (1989). The time course of sensory-specific satiety. *Appetite* **12**, 57–68.
- Holman, E. W. (1973). Temporal properties of gustatory spontaneous alternation in rats. *Journal of Comparative and Physiological Psychology* **85**, 536–539.
- Le Magnen, J. (1985). *Hunger*. Cambridge: Cambridge University Press.
- Lucas, F. & Sclafani, A. (1989). Flavor preferences conditioned by intragastric fat infusions in rats. *Physiology and Behavior* **46**, 403–412.
- Morrison, G. R. (1974). Alternations in palatability of nutrients for the rat as a result of prior tasting. *Journal of Comparative and Physiological Psychology* **86**, 56–61.
- Richman, C. L., Dember, W. N. & Kim, P. (1986). Spontaneous alternation behaviour: a review. *Current Psychological Research Reviews* **5**, 358–391.
- Rogers, P. J. (1990). Why a palatability construct is needed. *Appetite* **14**, 167–170.
- Rogers, P. J. & Blundell, J. E. (1984). Meal patterns and food selection during the development of obesity in rats fed a cafeteria diet. *Neuroscience and Biobehavioral Reviews* **8**, 441–453.
- Rogers, P. J. & Blundell, J. E. (1989). Separating the actions of sweetness and calories: effects of saccharin and carbohydrates on hunger and food intake in human subjects. *Physiology and Behavior* **45**, 1093–1099.
- Rolls, B. J., van Duijvenvoorde, P. M. & Rolls, E. T. (1984). Pleasantness changes and food intake in a varied four course meal. *Appetite* **5**, 337–348.
- Rozin, P. (1976). The selection of foods by rats, humans, and other animals. In *Advances in the Study of Behaviour*, pp. 21–76 [R. A. Hinde, C. Beer and E. Shaw, editors]. New York: Academic Press.
- Rozin, P. & Vollmecke, T. A. (1986). Food likes and dislikes. *Annual Review of Nutrition* **6**, 433–456.
- Sclafani, A. (1987). Carbohydrate taste and obesity: an overview. *Neuroscience and Biobehavioral Reviews* **11**, 131–153.
- Steiner, J. E. (1987). What the neonate can tell us about umami. In *Umami: a Basic Taste*, pp. 97–123 [Y. Kawamura and M. R. Kare, editors]. New York: Marcel Dekker.
- Strupp, B. J. & Levitsky, D. A. (1984). Social transmission of food preferences in adult hooded rats (*Rattus norvegicus*). *Journal of Comparative Psychology* **98**, 257–266.
- Treit, D., Spetch, M. L. & Deutsch, J. A. (1983). Variety in the flavor of food enhances eating in the rat: a controlled demonstration. *Physiology and Behavior* **30**, 207–211.
- Wurtman, R. J., Hefti, F. & Melamed, E. (1981). Precursor control of neurotransmitter synthesis. *Pharmacological Reviews* **32**, 315–335.
- Young, P. T. (1940). Reversal of food preferences of the white rat through controlled pre-feeding. *Journal of General Psychology* **22**, 33–66.