Voluntary food selection

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Summary

When they have a sufficient choice of foods, humans, pigs, poultry and ruminants all appear to be able to choose a composite diet that is close to optimal for their current needs. Their voluntary food intake (VFI) is the sum of the intakes of individual foods and is thus a consequence of their selection among foods.

Animals are innately apprehensive about novel foods but learn about them from mother, other adults and peers, or by cautiously testing specific foods and associating their post-ingestive consequences with their sensory characteristics. Foods (responses) can be categorised: unfamiliar (avoided); familiar but toxic (avoided); familiar, innocuous, but its nutrients not currently needed (indeterminate); or familiar with required nutrients (currently preferred).

Avoidance of a particular food (or supplement) can be through a conditioned aversion resulting from malaise due to toxins that stimulate the emetic centre. The animal learns to avoid the toxic food by associating that food's specific sensory characteristics (taste, odour, texture, colour) with the malaise. Inappropriate post-ingestive levels of circulating metabolites may also lead to negative stimuli and conditioned avoidance of the foods responsible, whereas positive post-ingestive stimuli may lead to conditioned food preferences. Thus, previous experience (familiarity) can profoundly affect the foods an animal selects or avoids when it begins a meal. Other homeostatic feedback signals may affect choice during a single meal. Satiety signals (eg. elevated hepatic carbohydrate oxidation rate, inappropriate concentrations of circulating metabolites) that target parts of the central nervous system other than the emetic centre may also lead to the cessation of ingestion of a particular food by an animal, even when it is not totally satiated.

Introduction

Maximising food intake in farm livestock is frequently considered to be a desirable goal, because higher feed intake generally leads to higher rates of production and usually greater economic efficiency. In humans, the concern is, usually, to reduce an excessive intake which leads to obesity. Much attention has therefore been directed towards elucidating the factors that control voluntary food intake, but less consideration has been given to the factors that enable animals to ingest balanced nutritious diets when given access to a number of different foods. This is understandable when animals are fed a 'complete diet' - formulated to provide balanced amounts of energy, protein and other nutrients (as occurs, for example, in the poultry industry) - but is not applicable to grazing animals, or penned animals fed loose mixtures of foods.

Blundell and Tremblay [1] argue that human nutritionists tend to be found in one of two disciplinary groups - either a school of energy balance (consisting of physiologists and biochemists) or a related school of eating behaviour (which has been considerably influenced by psychologists concerned about phenomena such as appetite and food preference or avoidance). The situation seems analogous amongst farm animal researchers. One school - apparently heavily influenced by the adage that 'animals eat for energy' - has focussed on animals' food consumption as being largely determined (started and stopped) by their internal energy status. Forbes [2] exemplifies this perspective as follows: 'Any attempt at formulating a more complex hypothesis [to explain intake control] must rely on energy as the principal commodity', although he is also in another school which has been more concerned to understand how animals make food choices based, for example, on nutrient status and learned associations between the sensory aspects of individual foods they have experienced and their post-ingestive and post-absorptive metabolic

consequences. The metabolic signals may be due to toxins, but also to circulating levels of amino acids, minerals and vitamins, as well as energy status.

These schools are, of course, not mutually exclusive. In recent years, feed intake research in farm animals seems, more and more, to be spanning the disciplines of psychology, physiology, biochemistry and nutrition. Emmans (3) has restated the earlier 'animals eat for energy' adage with an alternative: 'animals eat for the most limiting dietary component' which implies that animals exhibit a form of 'nutritional wisdom'. Although this concept has been controversial, it is of interest to re-examine this idea because humans and grazing animals usually have access to a range of foods from which to choose. Even penned livestock offered forages, long hays or grains may have at least some opportunity to select material of different nutrient composition from among the foods available to them. Thus it is not only how much food (and energy) an animal ingests, but what foods it selects from those available to it, that will determine its rate of growth, body composition and food conversion efficiency. How animals select foods from those on offer, and whether their choices are appropriate to their current nutritional needs, are thus central determinants of voluntary food intake.

Can animals make appropriate food selections?

We think that the answer to this question is an affirmative one. Evvard (4) characterised the intake of energy and nutrients by pigs which were offered unlimited access to a smorgasbord of familiar foods capable of providing a well-balanced diet. Notably, the diets chosen by the choice-fed pigs reflected modern feeding standards, and the pigs also voluntarily reduced their intake of protein-rich foods (and thereby the protein:energy ratio in their diet) as they matured. Some of the choice-fed pigs grew faster than had been previously reported for similar pigs fed the standard diet at the same research station.

Since 1916 much more evidence has accrued which shows that laboratory and farm animals normally make food choices that tend to optimise their growth potential. Emmans and Oldham (5) have reviewed this topic and proposed that what an animal chooses to eat from the foods on offer at any time is indicative of its striving to meet its current nutritional demands which are determined primarily by genotype. Genotype defines an optimal or 'preferred' pattern of growth and development, although the latter is seldom achievable because of environmental constraints. Nutritional demands, and thus the signals that determine phagic behaviour, may be modified by the animal's current physiological state as determined by ambient conditions, parasitism, disease etc.

There are numerous demonstrations that various animals - eg rats (6), chickens (7, 8), sheep (9), monkeys (10) and humans (11) - when offered a choice of foods that differ only in concentration of a single nutrient can, provided they have experienced those foods, select among them in order to meet their current requirements quite closely. At the same time, they minimise their intake of substances that would have led to non-specific nutrient imbalances, or toxicities. Pigs, for example, given a choice of two foods differing mainly in crude protein, content formulated their own diet in line with their decreasing requirement for protein relative to fat as they matured (12). In a similar way, sheep chose foods with a different protein content so that their mixed diet matched their current protein requirements while also avoiding an excessive intake of a rapidly degradable dietary protein source (9) or an excessive intake of a diet they associated with ammonia-induced malaise (13). Hills et al (14) have shown that ruminants selected between diets of higher and lower sulfur content in order to meet their presumed requirements while also avoiding excessive intake.

If it is accepted that animals as far as possible choose feeds in order to obtain sufficient energy and nutrients to support their genetically determined growth path (see 5), the question arises: how do they monitor and compare their internal state with the genetically defined 'ideal' state and then

appropriately adjust their feeding behaviour? In generating an appropriate food selection behaviour, is energy status a more important signal than that of amino acids, minerals or vitamins? Do animals totally avoid foods containing toxins?

How do animals make appropriate food selections?

It has been postulated that meal initiation, a prelude to any food selection, is the result of an integrated signal dependent on a reduction in the rate of hepatic oxidation of both glucose and fatty acids which is conveyed to the brain by the autonomic nervous system (2). When an animal is about to begin a meal, foods to which it has access can be seen as either 'familiar but known to be unsafe', 'unfamiliar and therefore potentially unsafe' or 'familiar and safe'. When selecting among different foods, animals choose mainly from the foods known to them (they are cautious about unfamiliar foods (and surroundings) or, in other words, they exhibit *neophobia*). This caution helps protect them from being poisoned. To overcome apprehension about novel foods (and surroundings), animals must repeatedly 'test' them in order to learn that they are non-threatening. Thus unfamiliar forage plants or supplements may not be consumed in significant quantities when they first become available, even though they could potentially make an important contribution to balancing the animal's diet.

Before weaning, lambs quickly become familiar with foods that are safe and nutritious by interactions with their mothers and other experienced animals (15). At all ages, they can also learn by a 'trial-and-error' process that depends on their sensing the metabolic consequences of testing particular foods (16). It seems clear they make associations between sensory attributes (taste, odour, texture, position) of novel foods and negative post-ingestive stimuli (malaise) and form conditioned aversions such that they subsequently reduce their intake of, or totally avoid, foods that cause malaise. Novelty of the food appears to enhance the association and strengthen the conditioned response (17). That these processes are at least partly non-cognitive is clear from experiments in which conditioned aversions to familiar foods have been produced by LiCl in rats (18) and sheep (19) during deep anaesthetisation.

When animals make appropriate food choices, it appears that, at times, both cognitive and affective processes are involved (see 17). The latter involve conditioned responses dependent on animals making an association between the taste (and smell) of the food eaten and some body-receptor-mediated response to the metabolic changes that follow ingestion, digestion and absorption of nutrients. In essence then, the animal optimises its metabolic environment by selecting foods whose positive attributes (provision of energy and essential nutrients) outweigh their negative attributes (energy cost of prehension, digestion and metabolism: presence of unwanted or toxic substances) so that, on balance, selection is directed towards foods providing an optimum supply of energy and nutrients that will enable the animal to develop according to its genetic potential.

Learning: conditioned aversion to toxins

Malaise occurring after a novel food is eaten, whether caused by natural food-associated toxins (17), by irradiation (20) or by certain drugs (21) will normally cause that food to be avoided later. In one study, pediatric cancer patients who were receiving nausea-producing chemotherapy drugs acquired a specific aversion to a particular novel ice-cream consumed immediately before undergoing chemotherapy (21). Likewise, sheep, pigs, poultry and rats acquire aversions to foods ingested in association with toxins that stimulate the body's emetic system. This system involves interactions between areas in the brain stem including the area postrema and the chemoreceptor trigger zone (see 17). That the emetic system is important in the formation of at least some types of aversion is further confirmed by the finding that administration of anti-emetic drugs attenuates the development of Li-induced aversions in sheep (22). Animals can form conditioned aversions based on associations with taste stimuli even when post-ingestive feedback

is delayed for many hours. Moreover, the strength of the aversion appears to depend on whether the food is novel, on the dosage of the aversive substance (eg LiCl) associated with the food, and the time between the ingestion of the food and the onset of malaise (17, 19).

Animals may be affected more adversely by toxins which are rapidly absorbed (eg alkaloids, 23; glucosinolates, 24). All animals have mechanisms for detoxifying and excreting unwanted metabolites, but the processes take time and the rate of ingestion of nutritious foods containing toxic materials may need to be restricted so that absorption and removal are approximately equal. Sheep given nutritious diets containing different concentrations of LiCl, reduce intake as toxicity increases, apparently to limit their intake of Li to a 'tolerable' level of 40-60 mg/kg liveweight (25). If the toxicity limit is reached for one food before the requirement for a particular nutrient is satisfied, it seems likely that the animal will then choose an alternative source of food containing the wanted nutrient, or choose smaller amounts of a wide variety of plants. Avoidance of toxicity may be one reason why ruminants select a varied diet.

Learning: conditioned aversions to nutrient imbalances

Aversions to foods can also be caused by normally non-toxic nutrients - eg an abnormal supply of propionate into the portal blood is aversive (26), probably because it affects metabolite flux in the citric acid cycle in liver cells and promotes metabolic acidosis. Thus, although high-energy diets enable ruminants to obtain nutrients rapidly (which is perhaps why they may show a preference for grain-based diets), they may nevertheless choose alternative foods while grain is available to them. This may be because the absorption of volatile fatty acids (VFA) or lactate arising from rapid rumen microbial fermentation of starch is causing mild toxicosis, or because other foods better fulfil current requirements.

An excess of protein in the diet can result in an unneeded level of ammonia or amino acid absorption. Normally the liver will convert an excess of amino acids to ammonia and a-keto acids with the ammonia then normally being removed via the urea cycle (albeit at a considerable energy cost). If ammonia absorption (eg. in ruminants given a urea supplement), or release during post-ingestive metabolism of unwanted amino acids exceeds the capacity of the liver to convert it to urea, intoxication may result from biochemical alterations in brain cells (27), which then could lead to a specific food aversion. The need to detoxify or remove energy or protein in excess of requirements may create a further metabolic burden - heat production - which has important consequences for food intake and production, especially in hot/humid environments. It would be interesting to know whether a high heat load in itself leads to specific conditioned food aversions. Ruminants consuming low digestibility, low nitrogen diets may absorb excess VFA relative to amino acids. Their sub-optimal food intake may be a consequence of the detrimental effects on intake of excess heat production caused by the animal's need to dispose of energy or nutrients which are out of balance with respect to requirements (28), and which may lead to the animal becoming averse to the foods available.

Bases for selection among familiar foods

An animal's 'dosage-related' intake of a food containing toxins provides only a partial explanation for why animals select among familiar foods. A related explanation suggests that excesses or imbalances of nutrients from certain foods may also stimulate the emetic system and induce conditioned food avoidance. Rogers and Egan (29) demonstrated that lambs became averse to foods producing amino acid imbalance and tended to avoid those foods when offered them later. It is possible that emetic pathways are involved in an animal's avoidance of foods that promote other nutrient imbalances.

Food avoidance based on conditioned aversion alone, however, does not appear to provide a complete explanation of how animals select a composite diet that meets their current requirements. If animals could form conditioned or learned <u>preferences</u> for foods (enabling the animal to

anticipate positive outcomes from eating particular foods), they could actively choose foods containing needed nutrients. This appears to be a more reasonable model than one in which animals passively ingest plants which they have learned were not excessively toxic when last ingested. Other mechanisms that provide contemporary feedback to the brain while ingestion is taking place may enable food selection to be 'fine-tuned'.

A relative excess of amino acids in the composite diet on the one hand or a relative insufficiency of carbohydrate or lipid energy on the other (ie an adverse protein:energy ratio in the absorbed nutrients) may stimulate the emetic centre and result in reduced intake of that food. Alternatively, an excess of certain amino acids may stimulate other parts of the central nervous system leading to a change in food selection. Anderson (30) has proposed a mechanism enabling animals to select for protein, based on associations between plasma concentrations of tryptophan or tyrosine and protein or energy intake, but did not provide evidence of a causal link. Forbes (2) points out that tyrosine concentration also affects catecholamine synthesis, and dietary tryptophan intake is correlated with 5-hydroxytryptamine concentrations in higher animals, both of which might affect dietary selection. Inadequate energy intake, which results in release of nor-adrenalin from the paraventricular nucleus (PVN), may increase the animal's preference for carbohydrate-rich foods. However, ingestion of carbohydrates stimulates the PVN to release serotonin which has has been reported to have the effect of reducing an animal's preference for carbohydrate-rich foods, and of increasing preference towards protein-rich foods (31).

The means by which a response to energy-nutrient imbalance is mediated is therefore not entirely clear. However, the brain stem, central nervous system, the neurotransmitter, serotonin, and other chemical messengers may be involved (see 17). In some instances heat load may also be a factor as discussed above.

Selection for specific nutrients

Animals have chemo-sensitive neurones in the area postrema which respond to glucose and osmotic pressure (32) and are thought to have receptors for amino acids; however, it is improbable that they have receptors for all essential nutrients (eg certain vitamins). Nevertheless, chickens requiring a source of thiamin to overcome an induced deficiency of this vitamin learnt to make an appropriate choice between a thiamin-containing, control diet and an otherwise identical thiamin-deficient diet (33). One explanation for such findings is that the intake of a nutrient-deficient food is reduced because animals develop acquired aversions to foods which lead to a metabolic imbalance (29, 17). An alternative explanation is that, in nutrient-deficient animals, ingestion of a food containing the deficient nutrient is reinforced by positive post-ingestive stimuli (a feeling of well-being) which then leads to a preference for that food (2). The precise mechanisms by which conditioned or unconditioned preferences are developed and mediated remain to be clearly defined.

Nutritional 'wisdom'

The extent to which ruminants can make appropriate food choices is exemplified by recent studies at Utah State University (34). Sheep given a choice between three feeds composed of the same ingredients but in different proportions could quickly identify the feed with the highest digestibility of energy (DE) even though the physical and nutritional differences were quite small (8.1-13.8% CP; 11.2-13.8 MJ DE/kg). Flavours (onion and oregano) were used to assist the sheep to discriminate between the foods but did not appear to much improve their discrimination in this study.

It was also noted that the sheep sampled at least a small amount of the 'lower quality' food on all occasions. In this connection, it has been widely reported that even when one food is ideally formulated, animals tend to choose a small amount of other available foods, even those that researchers presume to be of little nutritional value. This observation has been put forward as an argument against the animal's 'nutritional wisdom'. However, eating a variety of foods, in

general, gives a greater likelihood of a balanced diet and a reduced chance of over-consumption of particular toxins. There may also be a further benefit, in that the animal is in this way is continually testing its feeding environment, updating its knowledge of the foods available to it (which may themselves be changing in composition over time), and its ability to predict the post-ingestive consequences of foods potentially available to it.

When animals make appropriate food choices, it appears that, at times, both cognitive and affective processes are involved (17). The latter involve conditioned responses dependent on animals making an association between the taste (and smell) of the food eaten and some body-receptor-mediated response to metabolic changes that follow ingestion, digestion and absorption of nutrients. In essence, the animal optimises its metabolic environment by selecting foods whose positive attributes (provision of energy and essential nutrients) outweigh their negative attributes (energy cost of prehension, digestion and metabolism: provision of unwanted or toxic substances) so that, on balance, selection is directed towards foods providing an optimum supply of energy and nutrients that will enable the animal to develop according to its genetic potential.

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