Sensory and experiential factors in the design of foods for domestic dogs and cats

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The domestic dog (*Canis familiaris*) and the domestic cat (*Felis catus*) occupy an unusual position for those interested in diet selection. On the one hand, they are the only members of the Order Carnivora which are readily accessible for studies of food choice, which may then be extrapolated to their wild ancestral species. On the other, their adoption as pets in millions of homes worldwide has been paralleled by the growth of an increasingly sophisticated pet food industry, and concerted research into their nutritional needs (for recent reviews, see MacDonald *et al.* 1984; National Research Council, 1985, 1986; Edney, 1988). Studies of diet selection have accordingly focused both on the way that these animals obtain food in the wild (Turner & Meister, 1988), and on the mechanisms whereby they select between foods that are already available. The following review will concentrate on the latter.

CHEMICAL SENSES

Dogs and cats undoubtedly use both taste and smell in the detection and selection of food. The third chemosensory system, the vomeronasal organ, appears to be involved only in the perception of social odours (Hart & Leedy, 1987). There is a great deal more published information on the taste systems of the dog and cat, compared with that available on olfaction, and the space devoted to each reflects this disparity, rather than the importance of each sense in the life of either species.

TASTE

In the absence of psychophysical findings, information on the chemical stimuli which evoke taste sensations has come largely from studies of neurophysiology. Of the four cranial nerves which convey information on taste, only the facial nerve has been investigated in detail in either the dog or the cat. The roles of the other three nerves, the glossopharyngeal, the vagus and the trigeminal, can only be guessed at from a few published accounts (Kitchell, 1978) and comparisons with other species. Most studies of the facial nerve have used either the fibres of the chorda tympani, or the cell bodies of the geniculate ganglion; Boudreau *et al.* (1985) have concluded that all these studies have addressed the same taste systems, but unfortunately the various research groups have used different systems of nomenclature from each other, and have also modified their own terminologies from time to time. A summary of the equivalent taste groups in cat, dog and rat is shown in Table 1; it is readily apparent that the two carnivore species are basically similar. However, there are also important differences between cat and dog, particularly in the spectra of compounds to which each taste group responds.

Quantitatively predominant in both species is the amino acid system, which is most sensitive to a group of amino acids described as 'sweet' in man, including L-proline,

L-cysteine, L-ornithine, L-lysine, L-histidine and L-alanine. In the cat, the amino acid units are inhibited by a group of 'bitter' amino acids with hydrophobic side-chains (L-tryptophan, L-isoleucine, L-leucine, L-arginine and L-phenylalanine), and by some alkaloids (Boudreau & White, 1978). Cats prefer solutions of the 'sweet' amino acids, and reject the 'bitter' (White & Boudreau, 1975; Beauchamp *et al.* 1977). In the dog, the amino acids that are inhibitory in the cat are either neutral or stimulatory, with the possible exception of L-tryptophan (Boudreau *et al.* 1985). These units are also sensitive to sodium chloride and potassium chloride, in both dog and cat, and have probably been identified as salt units by some authors (Bartoshuk *et al.* 1971; Ishiko & Sato, 1973), but they have higher thresholds (>0.05 M) than typical salt units in other species.

A further and important difference between dog and cat is the sensitivity of the amino acid units to sugars. In the dog, a wide range of mono- and disaccharides, and some artificial sweeteners, are active, particularly D-fructose, β-D-fructose and sucrose, although the thresholds are higher than those of the most active amino acids (Boudreau *et al.* 1985). In the cat, neither this nor any of the other taste systems has been found to respond to sugars at any behaviourally-meaningful concentration (Boudreau, 1989). Cats are unable to distinguish between water and sucrose dissolved in water (Carpenter, 1956; Bartoshuk *et al.* 1971; Beauchamp *et al.* 1977), but prefer milk if sucrose or lactose is added (Frings, 1951; Beauchamp *et al.* 1977). Beauchamp *et al.* (1977) suggested that in the milk base, the cats might have been reacting to textural rather than taste cues (although an interaction between the sugar and the taste of other components in the milk cannot be ruled out); they were unable to replicate the preference for sucrose in 0.03 M NaCl reported by Bartoshuk *et al.* (1971). The latter result might be explained by a learned association between the physiological effects of the ingested sugar, paired with a taste cue from an impurity in the sucrose used, since the preference tests were carried out over 6 h. However, the ability of the cat to taste sugars directly is undoubtedly limited.

The acid units respond to carboxylic acids, phosphoric acids, and other Bronsted acids such as nucleotide triphosphates, histidine, histidine dipeptides, and protonated imidazoles. Some amino acids, such as the sulphur-containing L-cysteine and L-taurine, also trigger these units, while inosine monophosphate inhibits (Boudreau *et al.* 1985). Cat and dog units are generally similar. Cats reject medium-chain fatty acids (8:0) but not short-chain (MacDonald *et al.* 1985), which may indicate an interaction between the acid units and other neural groups.

The remaining taste groups in the facial nerve are less well characterized, but they consist of 'X-units', which display long latencies to electrical discharge, and discharge spontaneously in irregular bursts, rather than single spikes (Boudreau *et al.* 1985). In both cat and dog, all these units respond to nucleotide di- and triphosphates, but subgroups, often imperfectly defined, also respond to other compounds. In the cat, one subgroup is stimulated by a diverse range of substances, including quinine (hence, this group has been labelled 'bitter'), tannic, malic and phytic acids, and alkaloids. It may be these units, the amino acid units, or a combination of the two, which are responsible for the rejection of quinine by cats at a dilution a thousand times greater than that rejected by rabbits or hamsters (Carpenter, 1956). In the dog, a clearly-defined subgroup responds to a narrow range of sweet-tasting substances, particularly furaneol and methyl maltol. Boudreau (1989) considers that this type of unit is much more common in the glossopharyngeal nerve, and may, therefore, represent a major taste group for the dog.

Both cats and dogs are thought to have a 'water' taste, which appears to be based on

Table 1. *Summary of cat and dog taste groups in the facial nerve (geniculate ganglion), adapted from Boudreau (1986, 1989). (Alternative nomenclatures are from Boudreau & White (1978)* and Boudreau et al. (1985)†)*

Neural group	Cat	Dog	Rat	Man (psychophysical equivalent)
Amino acid (cat II, dog A)*	M	M	(m)	Sweet 1–bitter
Acid (cat I, dog B)*	M	M	—	Sour
Acid (rat type)	—	—	M	
Nucleotide (cat IIIA, dog C)* (type X)†	m	(m)	(m)	Umami 2
Furaneol (dog D)* (type Xb)†	—	m‡		Sweet 2
Bitter (cat IIIB)* (type Xb)†	m	—		
Salt	—	—	M	Salty

M, major group; m, minor group; (m), imperfectly defined; —, not detected.
‡ Probably more common in the glossopharyngeal nerve.

fibres, including acid-sensitive units, which discharge to pure water after they have become adapted to NaCl in the saliva (Bartoshuk *et al.* 1971). Tests of potential tastants in pure water may, therefore, be confounded by masking, due to the taste of the water itself.

Comparisons of these taste abilities with those of other species can indicate where adaptations to a carnivorous lifestyle have taken place. The most abundant units in the facial nerve of the rat, hamster and goat respond to salt; these units have not been detected in either dog or cat (Boudreau, 1989). However, there is very little information from either dog or cat on the taste information that may be transmitted through the glossopharyngeal nerve, and this must be borne in mind when considering negative evidence, particularly since a separate group of salt-sensitive fibres has been identified from the glossopharyngeal nerve in the rat. Amino acid units are uncommon in the rat, and respond to a different spectrum of amino acids; for example, the most effective is L-arginine, which is inhibitory in the cat and slightly stimulating in the dog. The response of rat 'acid units' is sufficiently different from those of cat and dog for Boudreau (1989) to classify them separately (Table 1). The nucleotide units have not been found in non-carnivorous mammals, but analogous systems are present in puffer fish (Boudreau, 1989), and some blood-sucking arthropods (Friend & Smith, 1977).

These differences between species are not easy to interpret in a nutritional context; for example, the way that the various taste groups are integrated in the brain is unknown, and species specificity at that level may be as important as differences in receptor function. However, the preponderance of amino acid units in dog and cat has been related to meat-eating, presumably to give them the ability to distinguish between meats of different quality. Monophosphate nucleotides, which accumulate after prey has been killed, are inhibitors of amino acid units in cats, and may regulate their feeding on carrion. The acid units may also be important in this context; at the pH of raw meat (5·5–7·0), carboxylic acids are not sufficiently ionized to stimulate these units maximally, and their sensitivity to the histidine dipeptides present in animal tissues may be more important. The response of these units to taurine may reflect the cat's requirement for this amino acid, but the dog, which does not have this requirement, shows an even

greater sensitivity to sulphur amino acids (Boudreau *et al.* 1985). The low sensitivity to NaCl in both cat and dog can be related to the high sodium content of much of their food. In the case of the dog, which will also eat a range of plant materials low in Na, the loss of this sense would appear to be maladaptive. The experimental evidence suggests that dogs can regulate salt intake, but that the associated physiological mechanisms are different to those in omnivores (Denton, 1982). The omnivorous habits of the dog may have led to the retention of both the sweet tastes seen in man, of which the furaneol group has been speculatively connected with fruit-eating (Boudreau, 1989). It can be speculated that the strictly carnivorous cat has refined both its amino acid and nucleotide systems to exclude potentially confounding signals from compounds characteristic of plant foods.

OLFACTION

Odour plays an important role in food selection; for example, when dogs were made anosmic with zinc sulphate, their ability to distinguish between types of meat was much reduced, while their preference for sugar was undiminished (Houpt *et al.* 1978). However, studies of odour perception, which have been more detailed in the dog than in the cat, have focused on the determination of thresholds (Moulton *et al.* 1960) and discrimination (Kalmus, 1955; Becker *et al.* 1957), rather than on the role of olfaction in food selection. There seems to be some plasticity in the link between odour and food, since meaty odours alone will not overcome neophobia in cats (Bradshaw, 1986) or sustain interest in a bland food for dogs (Houpt *et al.* 1978).

FEEDING BEHAVIOUR AND MEAL PATTERNS

The regulation of food intake appears to be distinctly different in the two species. Given free access to food, cats eat small meals, taken both day and night (Mugford, 1977) or only at night (Kanarek, 1975). Dogs tend to eat only during daylight (Mugford, 1977), and their feeding occasions are influenced by an endogenous rhythm (Ozon *et al.* 1986). Within certain constraints, to be discussed, cats can generally regulate their energy intakes, while some breeds of dog (e.g. beagles) tend to overeat by a factor of between two and five (Mugford, 1977), a habit which may be derived from the ability of wolves to gorge-feed on kills.

ROLE OF EXPERIENCE

Despite the effects of domestication, there is considerable evidence that both dog and cat have retained many of the abilities of wild mammals to respond to the nutrient content of their food, by altering their preferences. The need for this flexibility is obvious from the wide range of prey items taken by feral cats (Fitzgerald, 1988), and the omnivorous habits of dogs. Nutrient content is only one side of the cost–benefit equation for each meal; the costs of procuring the meal, in terms of energy expended, danger from predators etc., are minimal for a domestic or laboratory animal, but are real for feral and wild individuals. For example, in a survey of the feed preferences of house and farm cats, J. W. S. Bradshaw and D. W. Macdonald (unpublished results) found that the farm cats ate very little of a hard dry food when a food with high water content was available, and ascribed this difference to the longer 'handling' time required for the dry food.
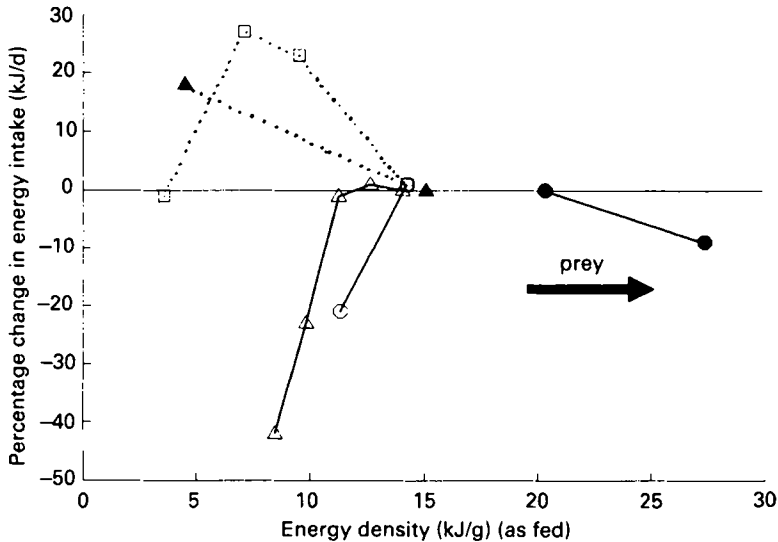
Fig. 1. Percentage changes in energy intake in five studies of cats fed on diets of different energy densities. (○), addition of cellulose (Kanarek, 1975); (●), addition of fat (Kane *et al.* 1987); (△), addition of kaolin (Hirsch *et al.* 1978); (▲), means of six commercial dry foods, and five commercial canned foods (Thorne, 1982); (□), dilution with water (Castonguay, 1981). (—), Changes mainly on a dry matter basis; (......), those mainly effected by changes in water content. ➤, The approximate energy density of prey items (MacDonald *et al.* 1984).

FLAVOUR EXPERIENCE

Previous experience of particular flavours can affect preference markedly, even when nutritional factors are controlled. Under different circumstances, novel flavours can either be rejected (neophobia) or preferred (novelty). The novelty effect is particularly persistent in puppies that have been fed on a single food for several weeks, but this type of dietary regimen has a similar effect on kittens (Mugford, 1977; Ferrell, 1984), adult cats (Hegsted *et al.* 1956; Thorne, 1982) and adult dogs (Griffin *et al.* 1984). Farm-to-farm differences in food preferences of feral cats have also been ascribed to novelty effects (J. W. S. Bradshaw and D. W. Macdonald, unpublished results).

Neophobia, to the point of food fixation, was induced in both puppies and kittens by Kuo (1967), but insufficient details were published to allow complete comparison between his trials and those mentioned previously. Breed may have an effect on the level of neophobia shown to various foods by puppies (H. Nott and C. J. Thorne, unpublished results). Attenuation of neophobia by exposure to flavour, but not by odour alone, has been demonstrated in adult cats (Bradshaw, 1986).

NUTRIENT EXPERIENCE

The greater prevalence of obesity in pet dogs than in pet cats (Anderson, 1974) indicates that cats are better able to regulate their energy intakes. However, trials to investigate the effect of energy dilution with celluflour or kaolin on food intake in cats have generally failed to demonstrate compensation (Kanarek, 1975; Hirsch *et al.* 1978). Increased intake of the low-energy foods used may have been inhibited by palatability factors, or it may be possible that the cat does not have the ability to discriminate

between energy levels that are well outside the range of those animal tissues (Kane *et al.* 1987). Compensation has been detected when water was the diluent (Castonguay, 1981), and when energy levels were increased using fats which were of high palatability (Kane *et al.* 1987). Using commercial cat foods with different water contents, Thorne (1982) found good evidence for energy regulation. Overall, the published evidence suggests that cats can only regulate their energy intake over quite a narrow range (Fig. 1), except that they can allow for changes in water content quite accurately.

Janowitz & Grossman (1949) concluded that dogs use bulk as the main cue for meal size; dilution of dog foods with cellulose resulted in sluggish and only partial compensation. Sugars added to drinking water did not result in any compensation of food intake by cats (Harrison *et al.* 1986), but glucostatic mechanisms in cats (Jalowiec *et al.* 1973) and dogs (Russek *et al.* 1980; Bellinger & Williams, 1989) appear to be different from those of the rat. Differences between cat and rat also emerged in a study of protein selection (Cook *et al.* 1985); kittens, unlike rat pups, did not learn to avoid protein-free diets, although they did appear to avoid taking more than 30% of their energy as protein.

EXPERIENCE OF TOXINS

The first symptom of a nutritionally-inadequate diet is often anorexia (e.g. thiamin deficiency in cats; Everett, 1944), probably induced by a learned dietary aversion to the flavour of the inadequate food. In cats, which are unable to digest high concentrations of sugars, an aversion to sucrose was detected 1 week after only 6 h exposure to a concentrated sucrose solution that induced diarrhoea (Bartoshuk *et al.* 1971).

Induction of aversions using lithium chloride has shown that cats may be more sensitive than dogs. Cats given a single meal of food containing LiCl refused to eat that food 3 d later, and showed a reduced appetite for the same food for at least 40 d, even though the test design involved repeated exposures to the same food unadulterated, and may, therefore, have accelerated the extinction of the aversion via 'learned safety'. The effects of LiCl could also be paired with the odour of the food alone (Mugford, 1977). Dogs, on the other hand, may be slow to learn, and quick to forget, the effects of LiCl; in one trial the dogs repeatedly ate the vomitus induced, and while they rejected the type of meat used to administer the LiCl for at least 7 h, after 24 h they would eat it once again (Rathore, 1984). However, long-lasting aversions resulting from the effects of LiCl have been demonstrated in coyotes (*Canis latrans*) (Quick *et al.* 1985), so variability in susceptibility to aversions is likely between canids, and possibly also between breeds of dog.

CONCLUSION

Even though specialized carnivores, such as felids, prey on 'nutritionally-exchangeable foods' (Rozin, 1976), both cats and dogs possess a sophisticated sensory capability, and the capacity to learn about the physiological consequences of their food. Thus, it is essential that commercial petfoods meet the highest standards for nutritional completeness and balance, as well as providing the animals with sensory variety. Compared with species more favoured by neurophysiologists and animal food psychologists, the mechanisms of diet selection in carnivores are still incompletely understood, but will continue to provide a fruitful area of study for behaviourist and nutritionist alike.

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