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How food preferences are learned: laboratory animal models

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Food selection represents a major challenge for omnivorous species. Faced with a variety of potential foodstuffs, many beneficial and some deleterious, the omnivore must decide which to eat and which to reject. The select–reject decision process involves an evaluation of the sensory characteristics of the foodstuff, particularly its flavour (i.e. taste, odour and texture). Innate predispositions such as a sweet-taste preference and bitter-taste aversion influence this process. With experience, animals refine their preferences as they associate the flavours of specific foods with the foods' post-ingestive consequences. Social interactions also contribute to the food choices of many animal species. Until recently, most research has focused on conditioned food aversions which readily develop when animals experience gastrointestinal malaise after eating a new food (Braveman & Bronstein, 1985). It is now well documented that strong food preferences can also be learned as animals experience the positive nutritive effects of foods. As reviewed below, a variety of models have been developed using laboratory rats to reveal the intricacies of food-preference learning.

CONDITIONED FLAVOUR-PREFERENCE PARADIGMS

The most common procedure used in the experimental study of acquired food preferences is the conditioned flavour-preference (CFP) paradigm. In one version of this paradigm different cue flavours (e.g. cherry and grape) are added to an energy food and a non-energy 'food' which can be in liquid or solid form. (To control for possible unlearned preferences for the specific cue flavours, the flavours paired with the energy and non-energy foods are counterbalanced across animals.) Rats are trained to consume the two flavoured foods during separate sessions to facilitate their associating the cue flavours with the post-ingestive consequences of the foods. Flavour-preference learning is then assessed in a two-choice test. In this test, the two flavours are presented in otherwise identical foods (e.g. a mixture of the energy and non-energy foods) so that any differential intakes can be attributed to a learned response to the two cue flavours. This training procedure is typically considered to be a form of Pavlovian conditioning with the nutrient being the unconditioned stimulus (US) and its associated cue flavour, the

conditioned stimulus (CS+); the flavour given with the non-energy food is labelled the CS-. (See Capaldi (1993) for other theoretical concepts of food-preference learning.)

There are several variations of this basic CFP paradigm. The US (nutrient) can be delivered by mouth, as described previously, or by a non-oral route (intra-gastric, intraduodenal or intravenous infusion). The US can be a nutritionally-complete diet, a specific macronutrient or even ethanol. The conditioned stimuli can be complex flavours which combine odours and tastes (e.g. artificial fruit flavours), specific tastes (e.g. sour and bitter) or specific odours (e.g. almond and vanilla odours). Animals can be trained under deprived (food and/or water) or non-deprived conditions and training sessions can be short (10–30 min/d) or long (23 h/d). Also, animals can be trained to associate different flavours with different nutrients (e.g. carbohydrate and protein) or different nutrient densities (e.g. high- and low-energy).

ORAL CONDITIONING STUDIES

The simplest and most natural way to condition flavour preferences is, as outlined previously, to add the cue flavour to the food source which the animal eats by mouth. This procedure (the oral-simultaneous method) mimics what normally happens when food is consumed. Using this training method, flavour preferences have been conditioned with various nutrients. For example, Mehiel & Bolles (1988) trained different groups of rats with flavoured (CS+) isoenergetic drinks containing sucrose, Polycose (hydrolysed starch), ethanol, or maize oil. On alternate days all groups were given a flavoured (CS-) non-nutritive saccharin drink; the CS+ and CS- flavours were lime and orange. In a subsequent two-choice test with the flavours presented in water, the four groups displayed similar preferences for the CS+ flavour over the CS- flavour. Since the nutrients differed in palatability, Mehiel & Bolles (1988) concluded that it was the post-ingestive consequences of the nutrients, not their flavour, that conditioned the CS+ preference.

Rats can also be trained to consume a CS+ (flavoured water) followed by the delayed presentation of the nutrient US (the oral-delay method; Holman, 1975; Capaldi *et al.* 1987a). For example, Elizalde & Sclafani (1990a) gave rats 10 min access to a CS+ flavour in water and then, after a 10 min delay, 30 min access to a maize oil emulsion (with no added flavour). On alternate training trials, a CS- flavour in water was available for 10 min followed by no nutrient. In the post-training choice test the rats showed an 80% preference for the CS+ flavour over the CS- flavour. Note that other rats trained with the CS+ flavour mixed into the maize oil emulsion (oral-simultaneous method) displayed a 94% preference for the CS+ flavour over the CS- flavour. Other studies, also, have reported that the oral-simultaneous procedure conditions stronger preferences than does the oral-delay procedure (Simbayi *et al.* 1986; Sclafani & Ackroff, 1994). Significant CS+ preferences have been reported with delays as long as 1–5 h between CS+ flavour and US nutrient (Elizalde & Sclafani, 1988; Capaldi & Sheffer, 1992). The ability of rats to acquire flavour preferences with delayed reinforcement is important because in the normal process of eating there is some delay between the orosensory experience and the post-ingestive consequences of food.

An interesting variation of the oral-delay conditioning procedure is to present the nutrient first, followed after a short delay by the CS+ flavour. Ordinarily, this 'backward' sequence (US→CS+) is not effective in Pavlovian conditioning but, with

nutrient US, flavour preferences have been reported using a US to CS+ delay of 3 min (Boakes & Lubart, 1988). This outcome, however, has been interpreted as a case of forward, not backward conditioning. That is, although the US is consumed first, its reinforcing post-ingestive consequences are not immediate, but rather may be experienced as the animal is consuming the CS+ flavour. In support of this view, flavour preferences are not conditioned if the US is presented 60 min rather than 3 min before the CS+ (Boakes & Lubart, 1988). A delayed reinforcing action may also account for the 'dessert effect' reported by Capaldi *et al.* (1987*b*). Rats trained to eat a potato 'course' followed by a sucrose 'dessert' subsequently showed a reduced preference for potato (relative to rice) than did rats that were trained with potato-only meals. Capaldi (1993) suggested that when sucrose follows potatoes, the flavour of sucrose is more closely associated with the post-ingestive reinforcing effects of potatoes than is the flavour of potatoes.

POST-ORAL CONDITIONING STUDIES

Another approach to study food-preference learning is to provide the nutrient via a route that bypasses the oral cavity. In this way, the flavour of the nutrient cannot interfere with the animal's learning to associate the CS+ flavour with the post-ingestive nutrient reinforcement. One common procedure is to pair the intake of flavoured water (CS+) with an intragastric (IG) nutrient infusion and the intake of a different flavoured water (CS-) with an IG water or saline (9 g NaCl/l) infusion. With the appropriate IG infusion variables, flavour preferences have been conditioned using complete diets as well as specific nutrients (glucose, Polycose, casein, maize oil, and ethanol; Holman, 1968; Puerto *et al.* 1976; Sherman *et al.* 1983; Baker *et al.* 1987; Sclafani & Nissenbaum, 1988; Lucas & Sclafani, 1989). However, preferences have not been obtained in all experiments, and in some cases, flavour aversions were conditioned by nutrient infusions (Deutsch *et al.* 1976). These negative results, however, do not detract from the positive findings, since the post-oral administration of nutrients can be problematic. Such infusions may be excessive in volume, rate and/or concentration and as a result may induce visceral discomfort (Booth, 1985).

It is not necessary to deprive rats to condition flavour preferences. Studies in my laboratory demonstrate that training non-deprived rats 24 h/d is very effective in conditioning flavour preferences. The animals in our experiments are fitted with two chronic IG catheters connected to two infusion pumps. Whenever the rats drink from one or two sipper tubes containing flavoured water the infusion pumps are automatically operated delivering nutrient or water to their stomachs at a rate approximating their oral ingestion rate. The rats are free to eat chow and drink fluid normally and they control the number and size of IG infusions they receive each day.

In our initial studies rats were trained by giving them one-bottle access, on alternate days, to a CS+ (e.g. cherry-flavoured water) paired with IG infusions of Polycose (160 or 320 g/l) and a CS- (e.g. grape-flavoured water) paired with IG water (Sclafani & Nissenbaum, 1988; Elizalde & Sclafani, 1990*b*). After 4 training days the animals displayed strong preferences for the CS+ over the CS- in two-bottle tests. Non-deprived rats also learn to prefer the CS+ flavour when it is paired with energetically-dilute infusions (10–40 g Polycose/l) and when the CS+ (paired with IG 320 g Polycose/l) and the CS- (paired with IG water) are concurrently available during training (Drucker

et al. 1993; Ackroff & Sclafani, 1994). These latter findings demonstrate the sensitivity of the post-ingestive feedback system that mediates flavour conditioning.

The pairing of the CS+ flavour with the IG nutrient infusion produces substantial and long-lasting changes in the rat's evaluation of the flavour. This is demonstrated first by the near-total preference (97–99%) rats displayed for the CS+ over the CS– with repeated testing (Elizalde & Sclafani, 1990*b*; Drucker *et al.* 1993). Second, rats continued to prefer the CS+ to the CS– for several weeks when the CS+ was no longer reinforced with IG nutrient infusions and after both flavours were not available for 1 month (Elizalde & Sclafani, 1990*a*; Drucker *et al.* 1994). That is, CS+ preference shows little or no extinction during the time-periods tested. Third, IG nutrient conditioning can convert an unpreferred flavour into a preferred flavour. Rats trained with a bitter- or sour-tasting CS+ solution (sucrose octa-acetate or citric acid in water) paired with IG Polycose infusions subsequently strongly preferred these CS+ solutions to plain water (Sclafani, 1991; Drucker *et al.* 1994). Untrained rats, on the other hand, preferred plain water to the bitter and sour solutions. Fourth, rats treat the CS+ as a food-relevant flavour. Drucker *et al.* (1994) reported that food deprivation selectively increased rats' intake of CS+ flavoured water, whereas water deprivation increased their intake of both the CS+ and CS– flavoured water. This response occurs even when the CS+ is no longer paired with IG nutrient infusions.

In addition to increasing the intake of a CS+ solution relative to a CS– solution (i.e. preference), IG nutrient infusions can also increase the absolute intake (acceptance) of the CS+ solution (Sclafani, 1991; Drucker *et al.* 1994). Ramirez (1994) reported the most striking case: rats given 24 h/d access to a saccharin solution paired with IG carbohydrate infusions drank 70% more saccharin than did rats given the saccharin solution paired with IG water. However, unlike conditioned preferences, the increased acceptance response does not occur with all cue flavours or IG nutrient infusions and it rapidly extinguishes when the CS+ is no longer reinforced with IG nutrient infusions (Drucker *et al.* 1994; Ramirez, 1994). Why nutrient conditioning more readily modifies flavour preference than flavour acceptance is not certain.

UNCONDITIONED STIMULI IN FOOD PREFERENCE LEARNING

Conditioned flavour preferences may be reinforced by both the orosensory and viscerosensory properties of nutrients. That is, rats may learn to prefer a cue flavour added to a nutrient source because they associate it with the palatable flavour of the nutrient (e.g. sweet taste of sugar) as well as the nutrient's post-ingestive consequences. This flavour–flavour conditioning has been formally studied by training rats with a cue flavour (the CS+) added to a palatable but non-nutritive solution (e.g. saccharin, mineral oil) which is now considered the US (Holman, 1975). For example, rats trained to drink a CS+ flavoured mineral-oil emulsion and CS– flavoured water subsequently showed a 78% preference for the CS+ when both flavours were presented in water (Elizalde & Sclafani, 1990*a*). This compares with the 94% CS+ preference displayed by rats trained with a nutritive maize-oil emulsion. Interestingly, flavour–flavour conditioning occurs only if the CS flavour is mixed with or immediately precedes the US flavour (Holman, 1975; Capaldi *et al.* 1987*a*). Thus, in the Elizalde & Sclafani (1990*a*) study cited previously, rats trained to drink CS+ followed 10 min later by a mineral-oil emulsion failed to develop a CS+ preference. Other rats reinforced with the delayed

presentation of a maize-oil emulsion, in contrast, showed an 80% preference for the CS+ over the CS-. Thus, flavour-flavour conditioning, unlike flavour-post-ingestive consequence learning is not possible when reinforcement is delayed.

Much remains to be learned about the post-ingestive sites and mechanisms of action by which nutrients condition flavour preferences. Deutsch & Wang (1977) proposed that nutrient receptors in the stomach mediate such conditioning but other investigators question this idea (Baker & Booth, 1989). Some findings indicate that intraduodenal nutrient infusions are as effective as intragastric nutrient infusions in conditioning flavour preferences, which argues against the stomach as a critical site (Blusk & Sclafani, 1993). The liver, also, has been proposed as an important site of action since hepatic-portal glucose infusions were found to be more effective than jugular infusions in conditioning flavour preferences (Tordoff & Friedman, 1986). It remains possible, however, that both pre-absorptive (intestinal) and post-absorptive (hepatic) detectors contribute to nutrient conditioning. Some evidence also suggests that both neural and hormonal feedback are involved in nutrient reinforcement. Horn *et al.* (1993) recently reported that selective gastric vagotomy blocks flavour conditioning by IG Polycose infusions, and injections of cholecystokinin and insulin were found to reinforce flavour preferences in some situations (Vanderweele *et al.* 1990; Pérez & Sclafani, 1991).

The nature of the post-ingestive reinforcing signals generated by nutrients is also an unresolved issue. Some investigators proposed that it is the satiating actions of nutrients that conditioned preferences (Booth, 1985; Rozin & Vollmeche, 1986), but various findings question this interpretation (Tordoff, 1991; Sclafani *et al.* 1993, 1994; Ackroff & Sclafani, 1994). Preference conditioning has also been attributed to 'energy' signals generated by nutrients (Mehiel & Bolles, 1988). More specifically, Tordoff (1991) hypothesized that nutrient reinforcement is mediated by signals generated by hepatic fuel oxidation. This is an attractive idea because it can account for the preferences conditioned by different nutrient classes as well as the effects of metabolic disruptions (diabetes) on preference conditioning. The findings of Tordoff *et al.* (1990) that rats preferred flavours paired with fructose over flavours paired with glucose was also taken as support for the hepatic fuel oxidation hypothesis because fructose is preferentially used by the liver. In subsequent work, however, we failed to confirm this result but observed instead that glucose conditions much stronger flavour preferences than does fructose in a variety of situations (Ackroff & Sclafani, 1991; Sclafani *et al.* 1993; Sclafani & Ackroff, 1994). Why, as our results indicate, the post-ingestive actions of glucose are more reinforcing than those of fructose remains to be established.

An argument against the notion that a common energy-related signal mediates preference conditioning is that it does not readily explain how animals can distinguish between different nutrients. Some findings indicate that rats can discriminate between the post-ingestive actions of nutrients and modify their food preferences accordingly (Piquard *et al.* 1975; Baker *et al.* 1987). We observed that rats can learn to associate one cue flavour with IG carbohydrate infusions and a different cue flavour with IG protein infusions (Pérez *et al.* 1994). When then given an IG protein preload before a choice test (with the two cue flavours paired with their appropriate infusions), the rats increased their preference for the carbohydrate-paired flavour. Similarly, an IG carbohydrate preload shifted the rats' preference to the protein-paired flavour. Conceivably, food preference learning may involve different types of post-ingestive signals, some nutrient-specific and some energy-related.

SOCIALLY-MEDIATED FOOD-PREFERENCE LEARNING

In the studies reviewed previously, flavour preferences were conditioned by the rats' individual experiences with nutrients. Rats can also acquire food preferences based on their interaction with conspecifics (Galef, 1991). Nursing is a common experience of all rats and can influence the rats' subsequent food choices. Several studies demonstrate that in feeding tests conducted outside the nest, rat pups prefer the diet consumed by their mothers (or foster mothers) over a novel diet (Galef & Clark, 1972; Galef & Henderson, 1972; Bronstein *et al.* 1975). This preference is mediated in part through flavour cues passed through the mother's milk (Le Magnen & Tallon, 1968; Galef & Henderson, 1972; Capretta & Rawls, 1974). For example, rat pups who nursed from mothers given daily injections of an odorant (citral) displayed a preference for citral-flavoured diet after weaning (Le Magnen & Tallon, 1968). Some studies indicate that flavour preferences can be influenced by prenatal sensory experiences. Pedersen & Blass (1982) reported that following prenatal exposure to an odorant (via *in utero* injection), rat pups preferentially attached to nipples coated with the odorant during their first suckling experience. Even more remarkable, rats given *in utero* exposure to a flavour (apple juice) showed an increased preference for that flavour as adults (Smotherman, 1982). The flavour cues need not be injected in order to have their effect: an enhanced preference for the odour of garlic (over onion) has been observed in rat pups whose mothers were given garlic during pregnancy (Hepper, 1988). These and other results demonstrate that the developing olfactory system is very responsive to odour cues which can result in long-lasting odour preferences (Leon, 1987).

The food choices of young rats are influenced also by sensory cues provided by adults at feeding sites. Young rats will eat more from a feeding dish with an adult rat nearby (even if the adult is anaesthetized) than from a feeding dish without an adult rat (Galef, 1981). Olfactory cues left by adult rats are sufficient to attract young rats to the feeding site (Galef & Heiber, 1976). Whether the presence of adults (or their odours) conditions a preference for the specific food at the feeding site is not known. Even if this is not the case, social cues, by stimulating young rats to eat food at a particular site, would initiate the flavour-nutrient conditioning process. Weanling rats given flavoured nutritive and non-nutritive foods rapidly learn to prefer the nutrient-paired flavour (Booth *et al.* 1974; Melcer & Alberts, 1989).

Social interactions can also influence the subsequent food preferences of rats. When offered the choice of two new flavoured diets, naive 'observer' rats that had previously interacted with a 'demonstrator' rat in the absence of food, preferred the diet that the demonstrator had just eaten (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983). This socially-induced diet preference can persist for several weeks or more, and can enhance the intake of normally unpreferred foods (Galef, 1989). Detailed analysis indicates that the socially-transmitted preference is not due to simple exposure to the flavour of food clinging to the fur of the demonstrator rat (Galef, 1991). Rather, the diet preference results from the observer rat's experiencing the flavour combined with olfactory cues emitted by the demonstrator rat. Carbon disulphide, a chemical found in rat's breath, has been identified as one of the olfactory cues involved (Galef *et al.* 1988). Socially-induced food preferences, therefore, may represent a special case of flavour-flavour conditioning where the US 'flavour' is the odour of the rat's breath.

Social cues provided by experienced conspecifics can significantly improve the nutritional 'wisdom' of rats (for review, see Galef, 1991). For example, naive rats given

the choice of a protein-sufficient diet and several protein-poor diets are more likely to select the sufficient diet if they had previously interacted with demonstrators who had eaten that diet (Beck & Galef, 1989). Also, naive rats are less likely to develop aversions to diets that demonstrator rats had eaten than to totally novel diets (Galef, 1987). Odour cues from demonstrator rats can also inform observer animals which of several distant sites may contain food (Galef, 1983).

CONCLUSIONS

Rats can acquire preferences for foods beginning at a very young age. Sensory cues provided by the mother both before and after birth can enhance the rats' preference for the mother's diet. Olfactory cues from conspecifics can induce preferences for other foods and direct rats to specific feeding sites. Rats will also learn food preferences based on their individual experience with new foods. The preferences for new flavours are enhanced when they are associated with already preferred odours and tastes. More importantly, rats readily associate novel flavours with post-ingestive nutritive consequences and develop strong and persistent preferences. They also appear capable of distinguishing the viscerosensory feedback provided by different nutrients, although relatively little is known about the physiological mechanisms involved. Thus, multiple learning processes contribute to the rats' selection of nutritious diets over the course of their lifetime. Although not discussed here, diet choices are also determined by ecological factors (e.g. food availability and acquisition costs) and ultimately animals must integrate their knowledge about the nutritional value of specific foods and the availability of these foods in the environment (Kamil & Sargent, 1981).

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REFERENCES

- Ackroff, K. & Sclafani, A. (1991). Flavor preferences conditioned by sugars: Rats learn to prefer glucose over fructose. *Physiology and Behavior* **50**, 815–824.
- Ackroff, K. & Sclafani, A. (1994). Flavor preferences conditioned by intragastric infusions of dilute Polycose solutions. *Physiology and Behavior* **55**, 957–962.
- Baker, B. J. & Booth, D. A. (1989). Preference conditioning by concurrent diets with delayed proportional reinforcement. *Physiology and Behavior* **46**, 585–590.
- Baker, B. J., Booth, D. A., Duggan, J. P. & Gibson, E. L. (1987). Protein appetite demonstrated: Learned specificity of protein-cue preference to protein need in adult rats. *Nutrition Research* **7**, 481–487.
- Beck, M. & Galef, B. G. Jr (1989). Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology* **103**, 132–139.
- Blusk, D. & Sclafani, A. (1993). Postingestive conditioning of flavor preferences from different infusion sites. *Proceedings of the Eastern Psychological Association Meeting* **64**, 42.
- Boakes, R. A. & Lubart, T. (1988). Enhanced preferences for a flavour following reversed flavour glucose pairing. *Quarterly Journal of Experimental Psychology* **40**, 49–62.
- Booth, D. A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: conditioned appetites and satieties. *Annals of the New York Academy of Sciences* **443**, 22–41.
- Booth, D. A., Stoloff, R. & Nicholls, J. (1974). Dietary flavor acceptance in infant rats established by association with effects of nutrient composition. *Physiological Psychology* **2**, 313–319.

- Braveman, N. S. & Bronstein, P. (editors) (1985). Experimental assessments of clinical applications of conditioned food aversions. *Annals of the New York Academy of Sciences* **443**, 1–441.
- Bronstein, P. M., Levine, M. J. & Marcus, M. (1975). A rat's first bite: The nongenetic cross-generational transfer of information. *Journal of Comparative and Physiological Psychology* **89**, 295–298.
- Capaldi, E. D. (1993). Conditioned food preferences. In *The Psychology of Learning and Motivation*, vol. 28, pp. 1–33 [D. Medin, editor]. New York: Academic Press.
- Capaldi, E. D., Campbell, D. H., Sheffer, J. D. & Bradford, J. P. (1987a). Conditioned flavor preferences based on delayed caloric consequences. *Journal of Experimental Psychology: Animal Behavior Processes* **13**, 150–155.
- Capaldi, E. D., Campbell, D. H., Sheffer, J. D. & Bradford, J. P. (1987b). Non-reinforcing effects of giving 'dessert' in rats. *Appetite* **9**, 99–112.
- Capaldi, E. D. & Sheffer, J. D. (1992). Contrast and reinforcement in consumption. *Learning and Motivation* **23**, 63–79.
- Capretta, P. J. & Rawls, L. E. III (1974). Establishment of a flavor preference in rats: Importance of nursing and weaning experience. *Journal of Comparative and Physiological Psychology* **86**, 670–673.
- Deutsch, J. A., Molina, F. & Puerto, A. (1976). Conditioned taste aversion caused by palatable nontoxic nutrients. *Behavioral Biology* **16**, 161–174.
- Deutsch, J. A. & Wang, M.-L. (1977). The stomach as a site for rapid nutrient reinforcement sensors. *Science* **195**, 89–90.
- Drucker, D. B., Ackroff, K. & Sclafani, A. (1993). Flavor preference produced by intragastric Polycose infusions in rats using a concurrent conditioning procedure. *Physiology and Behavior* **54**, 351–355.
- Drucker, D. B., Ackroff, K. & Sclafani, A. (1994). Nutrient-conditioned flavor preference and acceptance in rats: Effects of deprivation state and nonreinforcement. *Physiology and Behavior* **56**, 701–707.
- Elizalde, G. & Sclafani, A. (1988). Starch-based conditioned flavor preferences in rats: Influence of taste, calories, and CS-US delay. *Appetite* **11**, 179–200.
- Elizalde, G. & Sclafani, A. (1990a). Fat appetite in rats: Flavor preferences conditioned by nutritive and non-nutritive oil emulsions. *Appetite* **15**, 189–197.
- Elizalde, G. & Sclafani, A. (1990b). Flavor preferences conditioned by intragastric Polycose: A detailed analysis using an electronic esophagus preparation. *Physiology and Behavior* **47**, 63–77.
- Galef, B. G. Jr (1981). Development of olfactory control of feeding-site selection in rat pups. *Journal of Comparative and Physiological Psychology* **95**, 615–622.
- Galef, B. G. Jr (1983). Utilization by Norway rats (*R. norvegicus*) of multiple messages concerning distant foods. *Journal of Comparative Psychology* **97**, 364–371.
- Galef, B. G. Jr (1987). Social influences on the identification of toxic foods by Norway rats. *Animal Learning and Behavior* **15**, 327–332.
- Galef, B. G. Jr (1989). Enduring social enhancement of rats' preferences for the palatable and the piquant. *Appetite* **13**, 81–92.
- Galef, B. G. Jr (1991). Social factors in diet selection and poison avoidance by Norway Rats: A brief review. In *Appetite and Nutrition*, pp. 177–194 [M. I. Friedman, M. G. Tordoff and M. R. Kare, editors]. New York: Marcel Dekker.
- Galef, B. G. Jr & Clark, M. M. (1972). Mother's milk and adult presence: two factors determining initial dietary selection by weanling rats. *Journal of Comparative and Physiological Psychology* **78**, 220–225.
- Galef, B. G. Jr & Heiber, L. (1976). Role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *Journal of Comparative and Physiological Psychology* **90**, 727–739.
- Galef, B. G. Jr & Henderson, P. W. (1972). Mother's milk: a determinant of the feeding preferences of weaning rat pups. *Journal of Comparative and Physiological Psychology* **78**, 213–219.
- Galef, B. G. Jr, Mason, J. R., Preti, G. & Bean, N. J. (1988). Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. *Physiology and Behavior* **42**, 119–124.
- Galef, B. G. Jr & Wigmore, S. W. (1983). Transfer of information concerning distant foods: A laboratory investigation of the 'information-centre' hypothesis. *Animal Behaviour* **31**, 748–758.
- Hepper, P. G. (1988). Adaptive fetal learning: prenatal exposure to garlic affects postnatal preferences. *Animal Behaviour* **36**, 935–936.
- Holman, E. W. (1975). Immediate and delayed reinforcers for flavor preferences in the rat. *Learning and Motivation* **6**, 91–100.
- Holman, G. L. (1968). Intragastric reinforcement effect. *Journal of Comparative and Physiological Psychology* **69**, 432–441.

- Horn, C. C., Mitchell, J. C. & Martinson, F. A. (1993). The effects of selective vagotomy on conditioned flavor-nutrient preferences in rats. *Society for Neuroscience Abstracts* **19**, 816.
- Kamil, A. C. & Sargent, T. D. (editors) (1981). *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*. New York: Garland STPM Press.
- Le Magnen, J. & Tallon, S. (1968). Préférence alimentaire de jeune rat induite par l'allaitement maternel. (Feeding preferences of the young rat induced by mother's milk). *Comptes Rendus des Séances de la Société de Biologie* **162**, 387–390.
- Leon, M. (1987). Plasticity of olfactory output circuits related to early olfactory learning. *Trends in Neuroscience* **10**, 434–438.
- Lucas, F. & Sclafani, A. (1989). Flavor preferences conditioned by intragastric fat infusions in rats. *Physiology and Behavior* **46**, 403–412.
- Mehiel, R. & Bolles, R. C. (1988). Learned flavor preferences based on calories are independent of initial hedonic value. *Animal Learning and Behavior* **16**, 383–387.
- Melcer, T. & Alberts, J. R. (1989). Recognition of food by individual, food-naive, weaning rats (*Rattus norvegicus*). *Journal of Comparative Psychology* **103**, 243–251.
- Pedersen, P. E. & Blass, E. M. (1982). Prenatal and postnatal determinants of the 1st suckling episode in albino rats. *Developmental Psychobiology* **15**, 349–355.
- Pérez, C., Ackroff, K. & Sclafani, A. (1994). Carbohydrate- and protein-conditioned flavor preferences in rats: Effects of nutrient preloads. *Appetite* **23**, 317.
- Pérez, C. & Sclafani, A. (1991). Cholecystokinin conditions flavor preferences in rats. *American Journal of Physiology* **260**, R179–R185.
- Piquard, F., Schaefer, A. & Haberey, P. (1975). Effets de la perfusion de glucose, d'Acides amines ou de lipides sur le choix alimentaire chez le rat (Effects of glucose, amino acid or lipid infusion on dietary self-selection in the rat). *Physiology and Behavior* **15**, 41–46.
- Posadas-Andrews, A. & Roper, T. J. (1983). Social transmission of food preferences in adult rats. *Animal Behaviour* **31**, 265–271.
- Puerto, A., Deutsch, J. A., Molina, F. & Roll, P. (1976). Rapid rewarding effects of intragastric injections. *Behavioral Biology* **18**, 123–134.
- Ramirez, I. (1994). Stimulation of fluid intake by carbohydrates: interaction between taste and calories. *American Journal of Physiology* **266**, R682–R687.
- Rozin, P. & Vollmeche, T. A. (1986). Food likes and dislikes. *Annual Review of Nutrition* **6**, 433–456.
- Sclafani, A. (1991). Conditioned food preferences. *Bulletin of the Psychonomic Society* **29**, 256–260.
- Sclafani, A. & Ackroff, K. (1994). Glucose- and fructose-conditioned flavor preferences in rats: Taste versus postingestive conditioning. *Physiology and Behavior* **56**, 399–405.
- Sclafani, A., Cardieri, C., Tucker, K., Blusk, D. & Ackroff, K. (1993). Intragastric glucose but not fructose conditions robust flavor preferences in rats. *American Journal of Physiology* **265**, R320–R325.
- Sclafani, A. & Nissenbaum, J. W. (1988). Robust conditioned flavor preference produced by intragastric starch infusions in rats. *American Journal of Physiology* **255**, R672–R675.
- Sclafani, A., Nissenbaum, J. W. & Ackroff, K. (1994). Learned preferences for real-fed and sham-fed Polycose in rats: Interaction of taste, postingestive reinforcement, and satiety. *Physiology and Behavior* **56**, 331–337.
- Sherman, J. E., Hickis, C. F., Rice, A. G., Rusiniak, K. W. & Garcia, J. (1983). Preferences and aversions for stimuli paired with ethanol in hungry rats. *Animal Learning and Behavior* **11**, 101–106.
- Simbayi, L. C., Boakes, R. A. & Burton, M. J. (1986). Can rats learn to associate a flavour with the delayed delivery of food? *Appetite* **7**, 41–53.
- Smotherman, W. P. (1982). In utero chemosensory experience alters taste preferences and corticosterone responsiveness. *Behavioral and Neural Biology* **36**, 61–68.
- Tordoff, M. G. (1991). Metabolic basis of learned food preferences. In *Appetite and Nutrition*, pp. 239–260 [M. I. Friedman, M. G. Tordoff and M. R. Kare, editors]. New York: Marcel Dekker.
- Tordoff, M. G. & Friedman, M. I. (1986). Hepatic-portal glucose infusions decrease food intake and increase food preference. *American Journal of Physiology* **251**, R192–R196.
- Tordoff, M. G., Ulrich, P. M. & Sandler, F. (1990). Flavor preferences and fructose: Evidence that the liver detects the unconditioned stimulus for calorie-based learning. *Appetite* **14**, 29–44.
- Vanderweele, D. A., Deems, R. O. & Kanarek, R. B. (1990). Insulin modifies flavor aversions and preferences in real-feeding and sham-feeding rats. *American Journal of Physiology* **259**, R823–R828.