PLANT ANIMAL INTERACTIONS

How does pattern of feeding and rate of nutrient delivery influence conditioned food preferences?

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Abstract Ruminant herbivores have been shown to learn about food properties by associating food flavours with the food's post-ingestive consequences. Previous experimentation supporting the conditioned food aversion/preference hypothesis has generally employed very simple diet learning tasks which do not effectively represent the wide range of foods selected within single bouts typical of wild, free-ranging ruminant herbivores. We tested the ability of a ruminant herbivore to associate a food with artificially administered nutrient rewards in a designed experiment where we altered the temporal pattern of encounter with the food as well as the nature (fast or slow reward) of the post-ingestive outcome. Twenty-four goats were offered branches of Sitka spruce (SS) and Norway spruce (NS) for 4 h per day on two days per week for five weeks. The *pattern* of feeding varied with treatment such that the species on offer changed every hour (short) or every 2 h (long). The *energy* treatment altered the reward delivered during Sitka consumption so that animals were dosed either with pre-dominantly sugar (rapidly fermented), predominantly starch (slower fermentation rate), or with water (placebo). Preference was measured on the day following each learning day. We expected that goats would find it easier to associate SS with post-ingestive rewards when the duration of encounter was longest, and that associations would be stronger with the most rapidly digested post-ingestive reward. In the event, goats did not alter their consumption of SS in response to the treatments. Our results suggest that at the scale of temporal resolution of encounters with different plant species (1–2 h), and at the different rates of experiencing post-ingestive consequences tested in this experiment, ruminants do not appear to discriminate the nutritive properties of foods predominantly through a post-ingestive feedback mechanism. They must, instead, use a range of cues—including post-ingestive consequences—to assess food properties.

Keywords Post-ingestive effects · Diet choice · Feeding pattern · Ruminant herbivore

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Introduction

Free-ranging ruminant herbivores generally select a diet which is richer in nutrients and lower in toxins than the average available material (Arnold 1981; Illius and Gordon 1992). They may achieve this partly by preferentially selecting dietary components on the basis of colour, taste and texture using simple rules (Bazely 1990). For example, toughness of leaves is generally related to their content of lignin and hence indigestibility (Lucas et al. 2000), while greenness of leaves is correlated with nitrogen content (Bazely 1990). However, an emerging paradigm in the field of diet selection research is that ruminant herbivores learn

about the nutritional properties of foods by associating their post-ingestive consequences with their sensory properties (Provenza 1995). Thus, animals consume particular foods, experience positive or negative consequences as nutrients or toxins are absorbed, and subsequently learn to prefer those foods which deliver most nutrients or avoid those which lead to toxicity. In the case of nutrient conditioning, the development of preference in response to positive post-ingestive feedback has been shown to occur with a range of nutrient stimuli, including volatile fatty acids (Villalba and Provenza 1996), starch (Villalba and Provenza 1997) and casein (Arsenos and Kyriazakis 1999) when animals are given test foods in discrete feeding bouts and simultaneously infused with nutrient solutions.

The extent to which positive conditioning of this kind occurs in free-ranging herbivores is less clear. Browsing herbivores may include multiple species within their diet (Meuret and Bruchou 1994; Ramirez et al. 1997), and the task of associating particular foods with their post-ingestive effects becomes complex (Yearsley et al. 2006). It has been proposed that several foods ingested during short periods of time, all with different nutrient concentrations and mixed in the rumen, will decrease the probability of discrimination at the species level (Stephens and Krebs 1986; Van Wieren 1996). In previous work, we showed that when test foods were offered on different days and goats were dosed with positive, negative or neutral conditioning stimuli, animals were adept at discriminating which food had delivered which consequence when preference was measured (Duncan and Young 2002). When the same foods were offered simultaneously and the same post-ingestive stimuli were applied, animals were much less able to discriminate on the basis of positive and negative consequences. In our previous work (Duncan and Young 2002), we tested two extremes of a continuum: simultaneous vs. complete temporal separation of food types. In the current experiment we extended this work to quantify the duration of feeding bout required for animals to make associations between foods and consequences. Our first aim in the current work was, therefore, to test the prediction that:

1. The ability to discriminate between two foods, based on their differing post-ingestive consequences, will increase as the feeding bouts on single foods increase in length. Longer feeding bouts on a single food will allow animals to better associate a specific food with its post-ingestive consequences.

In addition to pattern of feeding effects on the development of conditioned preferences, it is possible that the rate at which nutrients are digested and absorbed may influence the ability of animals to make positive associations. The strength of behavioural responses depends on the temporal delay between stimulus (i.e. taste) and the reinforcer

(i.e. post-ingestive feedback) (Mazur 1994). Thus, one would intuitively expect readily fermentable carbohydrates which deliver immediate energy following ingestion to condition more robust preferences than slowly fermentable, fibre-rich foods. Our second aim was, therefore, to test the prediction that:

2. The ability to discriminate between two foods based on their differing post-ingestive consequences will be higher when nutrient rewards are experienced rapidly following food consumption than when more slowly available nutrient rewards are used.

Finally one might expect some interaction between length of feeding bout and the rate at which foods deliver nutrients. Thus, we would expect rapidly fermentable foods to be more successfully assessed in short feeding bouts than more slowly fermentable foods.

Our final prediction was, therefore, that:

3. Length of feeding bout and temporal delay in post-ingestive feedback interact: foods which provide a signal with a lag which is longer than the feeding bout will not be discriminated for or against.

Materials and methods

The experiment was conducted according to, and licensed under, current UK Home Office legislation.

Animals and diets

Twenty-four male Scottish Cashmere goats of approximately one year of age (live weight 26.5 kg, s.d. 3.65 kg) were individually penned indoors. The animals received a diet of dried grass pellets, straw and whole barley sufficient to satisfy maintenance energy requirements (MAFF 1975). Barley accounted for 30% of the energy intake, and straw was fed at a fixed daily amount of 100 g assumed to replace 50 g of the metabolizable energy supplied by the dried grass pellets. The diet was fed at approximately 15.00 h. The animals had unrestricted access to water throughout the day. The animals had no previous experience of feeding on conifer and other browse material.

Prior to the experiment, the animals were allowed to adjust to housing and handling for two weeks. In the second week, conifer material was introduced by offering one branch each (~200–400 g fresh matter) of Sitka Spruce (SS; *Picea sitchensis*) and Norway Spruce (NS; *Picea abies*) without time restriction from Monday to Thursday. On Friday, we conducted an initial preference test according to the procedures applied throughout the experiment. After the two pre-experimental weeks, the experiment was conducted for a further five weeks, during which the

animals were conditioned to feeds and post-ingestive stimuli on Tuesday and Thursday, with preference tests being conducted on Wednesday and Friday. Saturday to Monday acted as rest days.

Treatments

Feeding pattern

On conditioning days, beginning at 09.00 h, the animals were offered eight feeding bouts of either NS or SS in such a way that one conifer species was fed either for two or for four consecutive feeding bouts before the conifer species was changed (pattern treatment, Fig. 1). Therefore, both SS and NS were fed for four bouts on each conditioning day. Although each feeding bout nominally lasted 30 min, in practice the conifer material was removed and weighed after 15 min, to allow time for dosing, and no conifer material was available during the remaining 15 min. At each feeding bout a new branch of approximately 250 g fresh matter (mean 267 g, s.d. 117) was offered.

Starting species

Half of the animals were fed SS at the first feeding bout, while the other animals received NS (starting species treatment, Fig. 1). Both feeding pattern and starting species remained constant for each animal for the duration of the experiment.
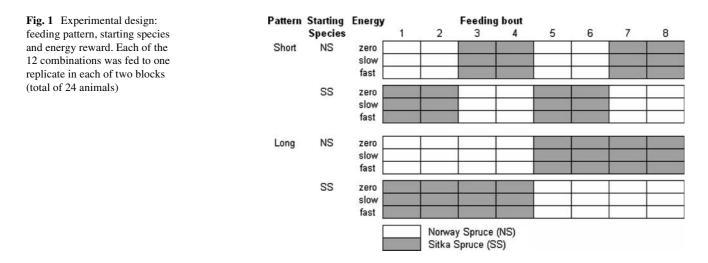
Energy reward

We determined the amount of conifer material consumed by weighing the branches immediately prior to placing them in the pens and reweighing them immediately after removal from the pens. We then orally dosed the animals with aqueous solutions of one of three different energy rewards (energy treatment) in proportion to the amount of material consumed. The three levels of the energy treatment consisted of water only (zero energy), and mixtures of sugar and maize-starch in the proportions of 1:4 (slow energy) and 4:1 (fast energy). Final strength solutions were mixed in such a way that they contained 4 g of substrate per 10 ml of solution. For each gram of fresh SS consumed, we administered 1 g of the respective solution. If the animals ate nothing during a particular feeding bout, the dosing gun was placed in the mouth but nothing was administered. During SS feeding bouts, animals were dosed 15 min after introducing a fresh branch. Dosing did not take place during NS feeding bouts.

During the first two weeks of the experiment the full dosing procedure was applied, but with water only for all treatments in order to establish a reliable measurement of baseline preference and to familiarize animals with the dosing procedure. In week three, the animals were dosed with 0.5 of the final concentration of the solutions. Full strength solutions were administered in weeks four and five of the experiment.

The experiment was designed with this two-week pretreatment period to allow within-animal comparisons to be made. Our previous work has shown between-animal variation in preference to be high and between-animal comparisons would have been much less statistically powerful than our chosen design. Furthermore, we have found that animals can make associations between foods and flavours based on post-ingestive consequences after only one or two encounters (Duncan and Young 2002) and that they are able to adjust preference in line with changing consequences, again after one or two encounters (Duncan et al. 2005).

Allocation of tree foliage to animals

The 12 combinations of the three factors (pattern × starting species × energy: 2 × 2 × 3) were each fed to two animals.

Fig. 1 Experimental design: feeding pattern, starting species and energy reward. Each of the 12 combinations was fed to one replicate in each of two blocks (total of 24 animals)

Because each tree only yielded a finite amount of foliage, we split the experiment into two blocks, each containing one replicate of each combination of factors. Previous work has shown that individual conifer trees differ in their concentrations of terpenes, and that this influences preference (Duncan et al. 1994). Because we knew about this source of variation and were not interested in it for the purposes of this experiment we deliberately confounded tree and day, offering conifer material from a single tree of each of the two species to animals of one block on each conditioning day and the accompanying preference test.

Preference tests

Preference tests were carried out each Wednesday and Friday by offering a branch of each species to each animal simultaneously for 15 min. Branches were accurately weighed before and after consumption to determine offtake. Animals were dosed immediately after preference tests according to their intake of SS as for the conditioning days to avoid confusing the association between SS consumption and post-ingestive consequences.

Conifer material

Immediately prior to the experiment, we collected foliage from Drumtochty Forest, Kincardineshire, with the permission of the Forestry Commission. For each conifer species, we selected 22 trees. We harvested enough material from each tree to provide sufficient feed for one conditioning day and the following preference test for one block of animals. The conifer material was sampled to determine dry matter (DM) and proximate nutrients, mimicking observed browsing behaviour. DM of SS averaged 49.8% (between-day CV = 12.2%) and DM of NS averaged 52.8% (between-day CV = 6.1%). Nitrogen, lignin, ADF and NDF values for SS were 0.98% (SE 0.037), 203 g/kg DM (SE 2.7), 400 g/kg DM (SE 6.1) and 495 g/kg DM (SE 5.7), respectively. Nitrogen, lignin, ADF and NDF values for NS were 1.04 % (SE 0.071), 188 g/kg DM (SE 4.2), 400 g/kg DM (SE 8.2) and 515 g/kg DM (SE 8.1), respectively. Foliage was stored at 4 °C for the duration of the experiment.

Validation of energy treatments using gas production technique

In vitro incubations with rumen fluid were conducted prior to the animal experiment to quantify the time course of fermentation of the energy substrates making up the two energy treatments. Gas production procedures in general followed the Menke method (Menke et al. 1979) with minor modifications. Pooled rumen fluid was collected from three rumen-cannulated sheep which had been fed the same ration as the experimental goats received during the main experiment for a two-week period. Because we were interested in the gas production in the first few hours of incubation, sensitivity was increased by increasing both sample size and amount of incubation liquid to 1.5-fold of that of the original method (300 mg DM sample size and 45 ml fluid, respectively). The amount of water introduced to the system by the aqueous sample solution (∼3 ml) was accounted for by decreasing the amount of water used when preparing the incubation liquid. Samples were transferred and weighed into the syringes using pipettes, while syringes were placed in an upright position on the scale. Blank samples were obtained by incubating 3 ml of water.

Six replicates of each of the three sample types (blank, sugar:starch 4:1, sugar:starch 1:4) were incubated. To account for the time lag between samples that occurred when adding the incubation liquid to the samples, blocks were formed containing one replicate of each sample. The order of samples within each block was assigned semi-randomly, assuring that any one sample type did not occur twice on the same position and that the order between any two samples changed as often as possible. Gas production was read every 20–30 min for up to 6 h and then less frequently until 48 h. Gas production of each sample was corrected for the gas production of the blank sample of the respective block before further analysis.

Statistical analysis

Preference test data were summarized for statistical analysis by calculating the amount of SS consumed during each preference test for each goat as a proportion of total intake for that preference test. These proportions were used to derive a covariate representing pretreatment preference values by averaging across the first four preference tests for each goat. Results of preference tests five to ten were then analysed by analysis of variance using goats as blocks. The main effects of energy, pattern and their interaction were estimated.

Conditioning day data were summarized by calculating the total amount of each species consumed over the 4-h conifer feeding period on each of the ten conditioning days. A covariate was calculated comprising mean intakes of each species for individual goats over conditioning days 1–4. Intakes for days 5–10 were then analysed by analysis of variance with treatment terms, species, energy, pattern and starting species. The block term included goat and conditioning day. This analysis demonstrated an overwhelming effect of species on intake. Further analysis of variance of conditioning data was therefore conducted separately for each species; otherwise the variance differed according to the species treatment.

Results

The gas production experiments confirmed that starch and sugar are fermented at very different rates in the rumen (Fig. 2). Both substrates yielded gas more-or-less immediately following addition of rumen fluid to syringes, but sugar was particularly rapidly fermented. The difference between fermentation rates was attenuated somewhat in the actual treatments used (maize:sugar 4:1 and 1:4), but differences were still readily apparent.

Goats much preferred NS to SS ($P < 0.001$). Average amounts of NS consumed during the 4-h conifer feeding periods for conditioning days 5–10 were around double the amount of SS consumed when adjusted for a pretreatment covariate (Table 1). The preference for NS was evident from the start of the experiment and did not vary greatly as the experiment progressed (Fig. 3). Similarly, the preference test data, expressed as the proportion of SS consumed relative to total intake during preference tests, confirmed a preference for NS; the mean proportion was 0.074 (SE, 0.0077), whereas in a no preference situation a proportion of 0.5 would be expected (Table 2).

The amount of SS and NS consumed during conditioning days was not influenced by the application of post-ingestive treatments ($P > 0.05$ for both energy and pattern treatments). Neither the energy treatment nor the pattern treatment significantly altered the amount of either species consumed (Table 1). The absence of treatment effects was confirmed by analysis of the amount of SS consumed as a proportion of total intake during preference tests (Figs. 4, 5). We would have expected treatment effects to increase this proportion upon application of treatments, but
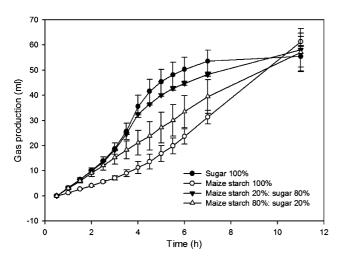
Table 1 Influence of energy and pattern treatments on the amounts of Sitka spruce and Norway spruce consumed during conditioning days (g fresh material)

			Energy			
			Fast	Slow	Zero	
Norway	Pattern	Long	571.1	637.3	579.4	596.0
		Short	591.5	591.0	605.0	595.8
		Mean	581.3	614.2	592.2	595.9
Sitka	Pattern	Long	182.8	215.4	187.8	195.3
		Short	207.3	191.7	200.5	199.9
		Mean	195.0	203.6	194.2	197.6

Values represent averages over conditioning days 5–10 and are adjusted for a covariate consisting of average amounts eaten by each goat during conditioning days 1–4. For mean values associated with Norway spruce consumption: SED for comparing overall energy mean values = 27.64; SED for comparing overall pattern mean values = 35.06; SED for comparing mean values within levels of energy or pattern = 49.43. For mean values associated with Sitka spruce consumption: SED for comparing overall energy mean values = 19.09; SED for comparing overall pattern mean values = 15.87; SED for comparing mean values within levels of energy or pattern = 27.49
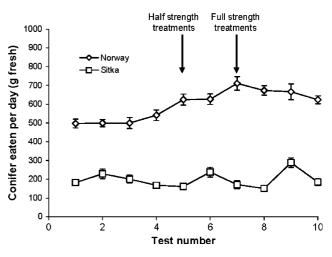

Fig. 3 Amount of conifer material (g fresh) eaten during 4-h feeding period during each of the conditioning days

our data show that application of treatments did not significantly alter the proportion.

Discussion

The results of our experiment suggest that at the timescale tested (1–2 h per feed type) goats were unable to correctly associate a test food with a positive nutritional stimulus dosed immediately after its consumption when the test food was immediately followed by a different food type. The duration of feeding on the test foods in our experiment was

Fig. 2 Gas production from in vitro rumen incubations with starch, sugar and combinations of starch and sugar in proportions reflecting the energy treatment. *Error bars* represent standard errors of mean values

Table 2 Influence of energy and pattern treatments on the amount of Sitka spruce consumed as a proportion of total intake during preference tests

			Energy			
			Fast	Slow	Zero	
Original data	Pattern	Long	0.0780	0.0412	0.0712	0.0634
		Short	0.0597	0.0729	0.1214	0.0847
		Mean	0.0689	0.0570	0.0963	0.0741
Transformed data	Pattern	Long	1.420	1.033	1.287	1.246
		Short	1.284	1.430	1.720	1.478
		Mean	1.352	1.231	1.503	1.362

Values represent averages over preference tests 5–10. For mean values of transformed data: SED for comparing overall energy mean values = 0.2714; SED for comparing overall pattern mean values = 0.2300; SED for comparing mean values within levels of energy or pattern = 0.3833
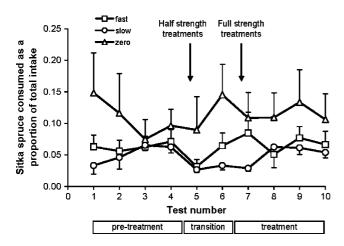

Fig. 4 Influence of type of nutrient reward on amount of Sitka spruce consumed as a proportion of total intake of conifer material during preference tests
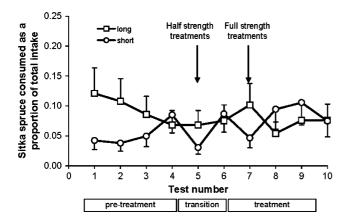

Fig. 5 Influence of pattern of feeding treatment on amount of Sitka spruce consumed as a proportion of total intake of conifer material during preference tests

relatively long compared to the time one might expect a foraging ruminant to consume a single food type. For example, in a recent detailed study of the ingestive behaviour of sheep, a single meal lasted around 2.5 h and included 13 distinct botanical species (Agreil and Meuret 2004). We chose our feeding durations by balancing what was logistically possible with what herbivores would experience in practice. However, even in our relatively straightforward feeding scenario we found no evidence that animals adjusted preference based on post-ingestive consequences.

One could argue that the animals did not respond to our post-ingestive stimuli because the signal was too weak. However, to put the amount of starch delivered into context, goats were consuming an average of around 200 g fresh SS per day by the end of the experiment, so we administered an average of 0.76 MJ ME in the form of starch to the animals on the slow treatment. Since the maintenance requirements of a 25 kg goat are about 4.5 MJ ME (Agricultural Research Council 1980), this is the equivalent of about 17% of ME requirements, which represents a considerable energy reward from consuming SS. Furthermore, in our previous work we have found that goats develop clear preferences for starch-associated feeds at equivalent reward rates (Duncan et al. 2006). Our animals were on a relatively low plane of nutrition relative to their requirements for growth. The background ration was designed to fulfil their maintenance energy requirements, but the animals were juvenile and thus still growing. Had they been given the opportunity they would have consumed at least double what they were offered based on intake predictions for growing ruminants derived from a meta-analysis of agricultural studies (Agricultural Research Council 1980). We therefore expected the experimental animals to be highly motivated to seek out energy rewards through their feeding behaviour, and the lack of response to our treatments therefore suggests that animals were unable to discern which food was offering energy rewards at the timescale tested.

A further question addressed by our experiment concerned the nature of the post-ingestive feedback. We hypothesized that rapidly digested substrates would yield more immediate post-ingestive consequences and so would be more readily associated with test foods than more slowly digested substrates. In the event, neither of our experimental energy substrates conditioned preferences to our test food. This was despite the fact that both energy substrates were probably more rapidly fermented in the rumen than would be the case for most plants consumed by browsing herbivores in natural situations. The gas production results showed that both substrates were rapidly fermented although the extent of fermentation was not great within the 1–2 h timescale of diet switching that we tested. The rate at

which nutrients alter post-ingestive signals that could be used by ruminant animals to assess food quality is not entirely clear from the literature; in some early work, increased portal blood concentrations of volatile fatty acids were detected within 15–30 min of commencing a meal (Chase et al. 1977), although in other work a much less direct relationship between feeding pattern and portal vein digestive metabolite concentrations was found (de Jong 1981). The possibility that animals can use chemoreceptors in the digestive tract to sense nutrients cannot be discounted. However, although it may be physiologically possible for ruminants to detect nutrients quickly and make associations with the food they are consuming at the time, our experiment suggests that this is not a primary mechanism by which animals judge food quality in multiple choice situations. Likewise, in a previous experiment (J.J. Villalba et al., unpublished results) groups of goats experiencing the temporal sequence of exposure to SS (*Picea sitchensis*) followed by exposure to Scots pine (*Pinus sylvestris*) or vice versa during: (1) extended, (2) medium or (3) short periods of time and subjected to infusions of starch: (1) immediately or (2) 20, 40 and 60 min after each offer of food did not develop preferences for the plant species as a function of either length of exposure to each food or rate of starch delivery to the rumen. A combination of pre- and post-ingestive cues must be necessary for animals to make correct assessments of food quality, and this has been suggested in previous research (Villalba and Provenza 2000; Ginane et al. 2005).

In terms of the implications of our study for understanding the role of post-ingestive consequences in shaping diet selection by browsing herbivores, we interpret our results as follows. Our results suggest that at the fine-scale resolution of diet choice typical of most natural habitats occupied by browsing herbivores, associations of food flavours with post-ingestive effects do not, in isolation, shape diet selection. At the feeding station and patch scale (Senft et al. 1987), animals would not experience particular food types for sufficient time to allow them to associate food flavours with consequences and alter their diet preference. At higher spatial scales, for example at the plant community or landscape scale, it is possible that animals could discriminate between broad food types and their associated nutrient rewards. However, it is likely that associations with post-ingestive effects work in concert with a range of other factors to help herbivores select appropriate diets. For example, it is possible that prior experience with the specific post-ingestive consequences of a food at higher spatial scales may then be used by herbivores to discriminate among plant species when subsequently confronted with choices at smaller spatial scales. Additionally, herbivores may also generalize cues learned at larger spatial scales to food attributes experienced while selecting foods at smaller

spatial scales. For instance, lambs that have eaten cereal grains such as sorghum, barley and wheat, all of which are predominantly composed of starch, subsequently prefer novel foods with added starch (Villalba and Provenza 2000).

The rate at which plant material is digested by ruminants is inherently slow because much of the energy derived from digestion of plants requires microbial action to break down structural carbohydrates. This timescale of energy release from plant material is not compatible with the much shorter timescale at which ruminant herbivores switch between different foods. The conditioned food aversion/preference hypothesis was derived from early work on rats. Rats are hindgut fermenters with distinct meal patterns; diet mixing is much less prevalent in rodents than in ruminants (Duncan et al. 2003). The transfer of ideas from the rat/psychological literature into the field of herbivore foraging ecology has been useful, but our results suggest that additional cues may be required to discern food quality in the complex habitats occupied by most ruminant herbivores. Our work suggests that the ability of ruminant herbivores to assess food quality primarily on the basis of post-ingestive consequences is limited at the scale of diet mixing typical of most of the habitats in which they forage. The mechanism of learning through post-ingestive feedback has been shown repeatedly in herbivores. However, the way that herbivores discriminate among several foods will also depend upon complementary mechanisms such as prior experience with food cues, generalization and novelty, which may contribute to strengthening specific flavour-post-ingestive feedback associations.

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