

MAIN LECTURE

Role of sensorial perceptions in feed selection and intake by domestic herbivores

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ABSTRACT - Sensorial perceptions play an important role in feed selection and intake by herbivores. Much research has been carried out to study the sensorial perceptions evoked by forages and their effects on intake and feed selection. Certain specific compounds are clearly able to evoke positive or negative sensorial perceptions when forages are eaten. This might lead to the development of plant extracts and aromas that might be used to improve the intake of unpalatable feeds. In the case of concentrates, the little research available seems to support an important role of the interaction between sensorial perceptions and post-ingestive effects when simple unmixed concentrates are supplied. It is not clear to what extent these effects are important when compound concentrates are offered. Despite these advances, it appears that most of the research carried out so far has been exploratory and observational. More research is needed to better understand the mechanisms underlying feed palatability before it can be included in intake prediction models.

Key words: Feed palatability, Feed preference, Ruminants, Herbivores.

Introduction - The role of some senses (i.e. sight, smell, touch and taste) in the feeding behaviour of herbivores has been the objective of extensive research. However, none of the published feed intake prediction models takes into account the sensory response to the feed as a factor (Baumont, 1996). This could be due to the fact that the effects of senses on feed intake regulation are not clear. Commonly, sensorial perceptions evoked by feeds are evaluated measuring their palatability. Greenhalgh and Reid (1971) defined palatability as the “dietary characteristics or conditions which stimulate a selective response by the animal”; thus palatability was considered as an inherent characteristic of the feed. Mertens (1996) distinguished between feed palatability and feed preference (or selection), defining the latter as a specific indication of palatability when the animal is given a choice. Although preference gives information about differences among feeds, it may not affect intake when a single feed is offered (Mertens, 1996). However, it is now accepted that the sensorial perceptions are modulated by the positive or negative post-ingestive effects that these feeds evoke to animals, based on their previous experiences. These experiences can occur early in life, such as prenatal or early growth stages (Simitzis *et al.*, 2008; Srinivasan and Patel, 2008) or during the productive life of the animals and are modulated by their requirements, strictly related with animals’ physiological status, and by external stimuli. They are memorized in specific areas of the brain cortex and when elicited by a sensorial perception

can induce reinforcement or aversion towards feeds, depending if previous experiences induced positive perceptions, i.e. feed reward, or negative ones (Provenza, 1995). Sensorial perceptions vary also within the same meal. As the meal goes on, initial strong sensorial perceptions evoked by the meal are attenuated by a series of anorexic neuro-hormonal signals, originated in the gastrointestinal tract, which send satiety signals to the nucleus tractus solitarius of the brain (Morton *et al.*, 2006). Thus, it seems more acceptable that palatability is defined as the interrelationship between sensorial and post-ingestive effects, influenced by feed's chemical and physical characteristics, animal's nutritional state and past experience with feed (Provenza, 1995).

Sensorial perception, diet selection and intake of forages - When a ruminant approaches a novel 'putative forage', after an immediate visual appraisal, which is usually quite inaccurate, olfaction is the first sense used as a gauge. In the case of forages, sensorial odorous sensations are often related to the presence and concentration of plant volatiles (PV) in plant parts such as leaves and stems, during the growth phase, as well as flowers and fruits, during the reproductive phase.

Plant volatiles belong basically to four compound classes (Pichersky *et al.*, 2006):

aliphatic compounds derived from the isoprenoid pathway (e.g. terpenes);

compounds containing an aromatic ring coming from the shikimic acid pathway, which can also result in the synthesis of lignin;

ternary compounds derived from decarboxilation and oxidation of fatty acids with synthesis of aldehyde and ketone moieties;

compounds containing N and/or S originated from the cleavage of amino acids, such as indole from triptophane.

These compounds are organic molecules of low molecular weight with a lipophilic attitude (Goff and Klee, 2006). In general the synthesis of PV is located in the epidermal layers of plant organs. Chemical composition, concentration and environmental emission of PV vary with plant species and varieties, plant tissues and organs, and plant physiological state. Environmental conditions such as edaphic features and climate may modulate these processes. In general forage species selection has favoured genotypes with a rather low concentration of these substances, virtually of no nutritive value and often potentially noxious to herbivores. However, as reviewed by Goff and Klee (2006), recent research has shown that PV often anticipate the presence of macro-molecules in the plant which are highly beneficial to animals' health (e.g. essential fatty acids, essential amino acids and pro-vitamins such as carotenoids). This is particularly true for flowers and ripening fruits, which tend to be attractive to pollinators and herbivores in order to favour fertilisation in the former and seed dispersal in the latter case, thus allowing species conservation. In vegetative organs, PV are often included in vacuoles and emitted to the environment only after tissue disruption. In this case, emission of PV is usually an aversive tool to defend the plant from attacks of fungi, insects and herbivores (Van Soest, 1994). Young leaves are often richer in PV than old leaves, with a concentration which usually increases with environmental harshness (e.g. low-fertility soils, drought). PV can also occur in plants due to contamination with animal faeces or attacks by fungi, which can mould forage tissue either *in vivo* or during forage conservation processes. These fungi produce exogenous PV responsible for the 'mouldy odour' often associated with presence of dangerous mycotoxins. Mouldy and dung-contaminated forages are usually refused by ruminants thanks to their olfactory perception. This is also the case for plants featured by highly repulsive endogenous odours (e.g. some bushes or trees, such as the carob tree branches, fully refused by sheep and goats as reported by Kaitho *et*

al., 1997). Refusal due to odour associated with post-ingestive effects can be used to condition the aversion towards toxic but relatively palatable plants (e.g. Landau *et al.*, 1999). If the olfactory evaluation step is successfully overcome, i.e. the smell of the plant is not so repulsive to prevent it from being eaten by the ruminants, the 'putative' forage is bitten off. If this occurs, during prehension, chewing, and swallowing a new sensation is formed as a result of the perception of the feed flavour (smell + taste) integrated with the somato-sensation related to the structure of the plant tissue bitten off.

Many studies have shown that specific plant compounds can alter diet selection and intake regardless of their nutritive value. Sweet taste associated with the presence of water soluble carbohydrates (WSC) has proved to boost preference for fresh or conserved grasses richer in these compounds in sheep (Dove *et al.*, 1999) and cattle (Smit *et al.*, 2006). Sugars are usually more abundant in grasses, whereas primary starch tends to accumulate in legume leaves and, particularly, stems. Cultivars of perennial ryegrass selected for a higher than average WSC content have, under some circumstances, enhanced intake and performance of growing sheep (Lee *et al.*, 2001) and lactating cows (e.g. Miller *et al.*, 2001). Siever-Kelly *et al.* (1999) demonstrated how much sheep like sugars in short-term cafeteria trials in which they unexpectedly ate more stems than leaves of chopped grass. This serious infringement of the general rule (leaves are usually preferred to stems) was related to the WSC-enrichment of stems via glyphosate spraying (98 vs. 240 g/kg DM of WSC in leaves and stems, respectively). Sulla stems rich in WSC are highly consumed by sheep (Molle *et al.*, 2003), increasing the coefficient of utilization in this forage (Douglas *et al.*, 1999). Besides depending upon plant genotype and plant parts, the concentration of WSC varies during the day and throughout the growth cycle. The circadian peak is usually in the early afternoon, when most of the daily photosynthetic process has already been completed (Orr *et al.*, 1997). According to several authors (e.g. Dove *et al.*, 1999) this pattern contributes to explain why sheep and cattle tend to graze more intensively in that period of the day. Numerous studies have shown that ruminants (Fisher *et al.*, 1999) and horses (MacKay *et al.*, 2003) prefer hay cut in the afternoon compared to that cut in the morning, even though the difference in sugar content is usually lower than 20g/kg DM. Whereas sugars have been proved to promote palatability of forages also via sensorial perceptions, many studies have shown the repulsive effects of compounds such as tannins on diet selection and intake, probably brought about to some extent by their astringency. Astringency is due to the immediate precipitation of proteins in saliva by the tannins, an effect whose intensity changes with tannins' structure and molecular weight. This 'astringency effect' is usually more abrupt in hydrolysable than condensed tannins (CT), whose role in controlling intake and dietary composition is probably more related to post-ingestive effects. This hypothesis has been supported by the decreasing circadian trend of preference for sulla, a legume containing a moderate concentration of CT (30-40 g/kg DM), in lactating sheep having free access to adjacent monocultures of Italian ryegrass and sulla during daytime (Rutter *et al.*, 2004). The mitigation of post-ingestive effects of condensed tannins by dosing an anti-tannic substance in the rumen (e.g. poly-ethylene glycol) effectively reduced the aversive effects of CT, thus increasing the intake and the preference for lentisk (20-25% CT on DM basis) in goats browsing a Mediterranean bushland (Decandia *et al.*, 2000).

Plant extracts from aromatic plants usually not foraged by ruminants or synthetic human food-flavoring agents have altered the preference and intake of forages, e.g. pelleted ammoniated straw (Robertson *et al.*, 2006) or hay (Distel *et al.*, 2007). In the former study, sheep and goats showed again a similar ranking of flavouring agents (with truffle, garlic, and onion being among the most preferred ones) with an enhanced intake of flavoured vs. unflavoured (control) straw.

Sheep were keener on flavours than goats. Distel *et al.* (2007) showed that the effect of flavouring on sheep preference depends upon hay quality, being higher in mid-quality (natural pasture hay) than high-quality (alfalfa hay) hays.

Much less literature has been devoted to the study of the effects of forage natural extracts on preference and intake. Dohi *et al.* (1996, 1997) succeeded in extracting a pool of flavouring agents from perennial ryegrass. The authors set up a method based on methanol solvent and were able to show that goats and sheep preferred grass hay sprayed with methanol extract of perennial ryegrass rather than control hay sprayed with water. Dohi *et al.* (1997) also demonstrated that sheep preference can be ascribed to the ethyl-acetate soluble fraction of the extract and, in particular, to the basic sub-fraction, which probably includes non-PV compounds (taste rather than odour boosting compounds). De Rosa *et al.* (2002) made up extracts from two forages (perennial ryegrass and white clover) using a different method of extraction (cold extraction in water). In cafeteria short-term trials the authors were able to enhance straw pellet preference in goats using the perennial ryegrass extract but not clover extract, confirming, under controlled conditions, the well-known higher preference of goats for grass than for legume previously demonstrated under grazing and short-term cafeteria conditions. In this study the effectiveness of the extraction process was preliminarily assessed by a panel test. Panellists were able to distinguish through triangle tests the aroma of the forages, their extracts and the flavoured pellets. In another cafeteria trial, neophobia towards rice bran (a low-value by-product) offered to sheep was effectively counteracted by spraying an extract of grass (flavoured bran) or just putting this extract below the trough (odoured bran) (Dam Van Tien *et al.*, 1999). The effect tended to increase along with adaptation. In contrast, the odour of dog faeces almost completely prevented bran intake, even after many days of adaptation.

Up to this point, focus has been given to on smell and taste sensorial perception, because these senses play a major role in ruminants when they are offered a novel feed. However, sight is also essential for an accurate association between a feed already known and the integrated sensation (sensorial plus post-ingestive) it can ultimately provide. Moreover, under grazing conditions, which are by far the most relevant for small ruminants, the visual location of watering points, grazing tracks and patches of different botanic composition are essential for setting up daily cues of feeding behaviour to tackle, as much as possible, the animals' requirements with an adequate menu of diverse feed resources (Meuret, 1996).

The case of horses. Visual appreciation of forages for the horse is a matter of concern due to its anatomy (lateral-positioned eyes; Fraser, 1992) and its relative blindness to some colours (e.g. green and yellow; Macuda and Timney, 1999) which humans perceive as a major criterion to distinguish young (high value) from old (low value) forages. Moreover, horses cannot easily visually appreciate feed which is far above ground level (even at 70 cm. a.g.l.; Hall *et al.*, 2003), what makes them worse browsers than ruminants under free-ranging conditions.

Despite the above handicaps, horses have been able to evolve as grazers to date thanks to their fine oro-sensory capacity. In fact this is regarded as one of the major driving factors of intake and dietary selection in this species, at least for two main reasons:

the fill-control of intake in these herbivores plays a minor role as compared to ruminants. Horses digest less effectively than ruminants (e.g. from -2 to -7 points of DM digestibility in horses than sheep, depending on the forage quality) and have a shorter transit time, since they can excrete 3-6 times bigger undigested fiber fractions than those excreted by cattle of similar body size (Dulphy *et al.*, 1995);

the metabolic control is probably of less relevance for horses than for ruminants because i)

horses forage during a longer period of the day: Harris (1999), quoted by Thorne *et al.* (2005), reported 18 h/day in grazing horses; Dulphy *et al.* (1997) found that, under stall-feeding with forage-based diets, 754 min vs. 278 min daily were devoted to foraging in horses and sheep, respectively, with a double number of daily meals – 12 vs. 6 – in the former than in the latter species; ii) even in saddle or race horses with relatively high energy requirements and level of nutrition, hay usually represents at least 30% of horse diet and the number of daily meals, especially for concentrates, is rarely below 3 (NRC, 2007). In general, diets for horses have lower energy and protein concentration than diets for high performing cows of the same metabolic weight, in which the time for feeding is constrained by the time required for rumination.

In contrast to other herbivores, particularly under the above mentioned conditions (i.e. individual feeding in stable), the sensory-specific satiety (Rolls, 1986, cited by Thorne *et al.*, 2005) is very important for horses, beyond the nutrition *per se*. In fact, horses kept in stable and fed adequate but monotonous diet often tend to develop non-foraging stereotyped 'frustration behaviours' (e.g. pawing, stereotypic weaving) and tend to enhance the intake of straw from bedding, which is regarded as risk factor for the occurrence of colics. These are indicators of below-optimum welfare conditions and, in the long run, may negatively affect horse performance. It must be pointed out that these abnormal behaviours are not just feed driven, since they are also related to a lower than optimum level of exercise and overall to a low level of social relationships. Nevertheless, enriching the diversity of the diet in horses fed under these conditions, by offering low amounts of various feedstuffs (hay, haylage and roots such as swedes and carrots; Goodwin *et al.*, 2002) or by adding diverse flavouring agents to low-energy concentrates (Goodwin *et al.*, 2005b) or cereal-byproduct meals (Goodwin *et al.*, 2005a), has effectively, although probably partially, counteracted the stressing conditions mentioned above, thus reducing the non-foraging stereotyped behaviours and the foraging time on straw. Overall, horses tended to spend more daily time foraging on diverse diets than on monotonous ones. In the case of diverse diets, they sampled all feedstuffs on offer, showing a partial preference, among hays, for molassed alfalfa chaff and short- rather than long-chopped hays, among roots, for carrots (Goodwin *et al.*, 2002) and, among flavouring agents, for fenugreek followed by banana, cherry, rosemary, cumin, carrot, peppermint and oregano (Goodwin *et al.*, 2005a). Moreover, the enrichment of the environment by odours and flavours from diverse feeds was successfully applied over a longer period (1 week) than the usual cafeteria tests, suggesting that this feeding management can be regarded as a beneficial and practical tool, even in the long run (Thorne *et al.*, 2005).

Sensorial perceptions, palatability and preference of concentrates – The palatability of concentrates has been little studied. Despite this, it is quite common to observe they are refused when some ingredients of concentrate mixes are changed. This occurs more frequently when they are supplied separately from forages, e.g. during milking.

One of the few studies available is that by Quaranta *et al.* (2006), which compared in Merino lambs the palatability (one feed by time in 30 min tests in experiments replicated in two periods) and then the preference (all feeds available together) of 11 concentrates and of alfalfa pellets. The results of the palatability tests suggested a marked neophobia (i.e. refusal of unknown feeds) for several feeds in the first period and a quick learning process in the second, probably associated to strong post-ingestive effects caused by the length of the tests. The rank in DMI among the feeds was also different in the two periods. The preference test showed that the rank of feed preference was uncorrelated with that observed in the palatability tests. This probably because when allowed to choose among feeds (preference test), the animals tried to eat a balanced diet

and to avoid deficiencies, thus choosing a mix of feeds (Quaranta *et al.*, 2006). This highlights that in this experiments post-ingestive effects played a major role.

With the aim of studying sheep sensorial perceptions, our research group evaluated the palatability of concentrates in short duration tests immediately followed by the supply of a grass hay, to reduce the post-ingestive effects and confound the animals on the feeds that evoked them (Mereu, 2009; Mereu *et al.*, 2009c). All feeds tested were finely ground to reduce the influence of texture on feed choice and, possibly, to increase their aromatic cues. Thus, 13 concentrates and dehydrated alfalfa were subjected to 6-min palatability tests, supplying one feed only per each test to 14 female lambs (inexperienced animals) and 14 multiparous dry ewes (experienced animals), in two Latin square experiments. The animal received each feed only once during the whole experiment. The results showed that the differences in intake between the most and the least preferred feeds were very large (Table 1), demonstrating that sensorial perceptions can have important effects in practical terms. Many animals refused even to taste certain feeds, suggesting an important effect of smell in feeding choices. In particular, dehydrated alfalfa, oat grains, canola meal, and sunflower meal were the most refused by both lambs and ewes. The DMI of lambs during the tests varied from high to low values in a continuum, as if the novelty of the feedstuffs under study pushed them to explore most of feed options but also to refuse those feeds that induced negative, possibly innate, sensorial perceptions. In contrast, the ewes had a marked preference for 4 feeds often supplied as single ingredients (beet pulps, wheat grains, pea grains, and corn grains) and low intake or complete rejection of the remaining feeds, including several commonly used in sheep feed mixes but rarely supplied alone. This suggests that previous feeding experience had a major role in their sensorial perceptions and evoked a conservative behaviour. In other words the ewes were not prone to eat novel feeds, even those generally considered very palatable, such as soybean meal.

In the same research, two of the most unpalatable feeds, canola meal and oat grains, were used to study if their palatability by lambs and mature ewes could be enhanced through the addition of flavours (Mereu, 2009; Mereu *et al.*, 2009a,b). Two Latin square experiments were carried out to evaluate the palatability of canola meal (1st experiment) or oat grains (2nd experiment) fed alone (control) or combined with 13 different flavours, formulated to elicit sweet (8 flavours), umami (4 flavours) or bitter (1 flavour) tastes. Each animal received only once each feed + flavour combination but all combinations included the unpalatable feed. The results showed that the DMI in the 6 min tests increased for almost all feed + flavour combinations as the experiments progressed, suggesting that the animals eventually adapted to the initially unpalatable feed present in all combinations. Some flavours (mostly sweet-based flavours) seemed to favour the adaptation of the animals to initially unpalatable feeds, reducing the variability of DMI among animals. Another important finding was that the ewes showed a faster learning process, as the experiment progressed, towards a relatively new feed than the lambs, as if ewes were more responsive to the post-ingestive effects of the diets or more able to identify the feeds used even when flavours were added to them. Whereas the ewes seemed to be able to eat large amounts of the two feeds initially perceived as unpalatable as they became acquainted with them, the lambs adapted to canola meal but maintained a strong aversion for oat grains.

The 14 feeds were analyzed by gas chromatography olfactometry and mass spectrometry to determine their aroma profile and to identify the chemical families associated with intake responses (Rapisarda *et al.*, 2009). The results suggested that for several feeds the short-term choices of the animals could be associated to specific chemical families. For example, the occurrence

Table 1. Percentage of animals that refused the feeds and mean DMI of each feed supplied to lambs and ewes during the 6 min tests (Mereu, 2009).

Feed	Lambs		Ewes	
	% lambs that did not eat	DMI, g in 6 min	% ewes that did not eat	DMI, g in 6 min
Beet pulps	29	11.9 ^{abcd}	0	62.8 ^a
Canola meal	43	5.0 ^{bcd}	43	2.7 ^b
Corn gluten meal	29	1.7 ^{cd}	0	14.8 ^b
Corn grains	0	14.9 ^{abc}	7	52.7 ^a
Corn middlings	14	7.5 ^{bcd}	14	18.0 ^b
Dehydrated alfalfa	71	0.4 ^d	50	1.5 ^b
Oat grains	50	0.0 ^d	14	9.8 ^b
Pea grains	7	17.4 ^{ab}	0	56.3 ^a
Soybean hulls	21	13.1 ^{abcd}	36	6.3 ^b
Soybean meal 44	14	10.9 ^{abcd}	29	7.1 ^b
Soybean meal 49	14	24.5 ^a	50	3.8 ^b
Sunflower meal	29	2.8 ^{cd}	7	6.2 ^b
Wheat brans	14	11.4 ^{abcd}	7	18.6 ^b
Wheat grains	21	22.8 ^a	0	56.4 ^a

^{a,b,c,d}Letters indicate differences within columns for DMI ($P < 0.05$).

of volatile sulphur compounds seemed to influence negatively the palatability of the tested feeds in both lambs and ewes. The same probably applied to terpenes with reference to the palatability of oat grains. However, more research is needed to better understand which specific compounds are involved in sensorial perceptions and to what extent their effects on palatability are innate or acquired.

Conclusions - Sensorial perceptions play an important role in feed selection and intake by herbivores. Much research highlighted the interactions between sensorial perceptions and post-ingestive effects evoked by forages. In the case of concentrates, the little research available seems to support an important role of sensorial perceptions on their intake, especially when supplied unmixed. Despite these advances, it appears that most of the research carried out so far has been exploratory and observational. More research is needed to better understand the mechanism underlying feed palatability before it can be included in intake prediction models.

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