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Methods for assessing taste abilities and hedonic responses in human and non- human primates

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Introduction

As a primary interface between an organism and the alimentary environment, the taste system is a major part of the biological background from which feeding behaviour and food habits have developed. Accordingly investigating taste abilities helps understanding both the former interaction that shaped the present human status, and how the socio-cultural parameters presently interferes with such a background. In the evolutionary perspective, non-human primates provide a reliable model for the study of the relationships between food choices and taste abilities. The large variability of human feeding behaviour must be investigated starting from that biological basis and its possible variation in different human populations, before assessing cross-cultural variation.

Taste parameters

Most studies on taste abilities have focused on three main parameters: taste quality, taste intensity and pleasantness/unpleasantness. In taste tests, the use of pure compounds in solution allow to focus on the gustatory component of the taste sensation. But one should note that taste sensation elicited by food generally involves a multimodal sensory response including taste, olfaction, and touch. This global perception results of the convergence between taste and olfactory processing into the brain cortex (Rolls, 1997). It is not intended to provide an exhaustive review of methods applied to characterise human taste perception, given the plethora of methods (Bartoshuk, 1978; Meilgaard et al., 1987). Instead only basic methods, relevant to the topic of sensory anthropology, will be presented.

Gustatory perception is usually assessed by a measurement of taste thresholds (i.e. the minimum perceived concentration of a taste stimulus) and supra-threshold taste responses (perceived intensity and hedonics). This involves distinct methodological approaches in non-human primates and in humans.

Methods for Studying Taste in Nonhuman Primates

In primates, the recording of taste responses is based on a spontaneous choice of the provided solutions. Accordingly, the taste response is necessarily global, including recognition altogether with acceptance/rejection of the stimulus, at the threshold and above the threshold.

The procedure designed for determining taste threshold in primates, the two-bottle test, has been initially used by Glaser (1968), following the pioneering work of Richter & Campbell (1939) on rodents. A solution of a compound (for instance sucrose) is presented simultaneously with a bottle of water, and the spontaneous consumption of each liquid is recorded. Various concentrations of the compound are presented, up to a lower limit (when there is no difference in the consumption of water and tested solution).

This procedure has been modified by Simmen and Hladik (1988), using a random presentation of the various concentrations and applying a statistical test (paired-sample *t*-test) to determine the lowest concentration for which a significant difference of consumption occurs. The time of each test is limited to a short period (ranging from a few minutes to three hours, according to the substance and the species body weight), because long-term post-ingestive effect might affect ingestive response, especially when testing sugar solutions; and the test should be performed before the animals are fed with their daily meal.

The position of the two bottles must be varied at random during each trial, to avoid a side-preference effect, especially during a period of shaping at the beginning of the test. Tests are started after completing a period of habituation during which the individuals are supplied with a high concentration of sugar solution and tap water simultaneously. Habituation is considered achieved when a marked preference for the sweet solution is recorded over 4 successive trials.

This type of test can be used for both attractive substances (sugars) and distasteful compounds (such as quinine or tannins); however, using the latter type to determine taste rejection thresholds necessitates to maintain the animal's motivation by providing, alternately, a sweet solution at supra-threshold concentration. An alternative protocol for distasteful compounds is to mix the tastant with a moderately sweet solution (twice the threshold), to be provided simultaneously with the same sweet solution, instead of water instead of water (Simmen et al. 1999). This procedure is particularly appropriate for tannin solutions, which are subject to oxidation, as it reduces the duration of the tests.

Such thresholds, although determined with a behavioural method (that could imply weak responsiveness to low concentrations) have been compared with the sensitivity of peripheral nerve of the taste system. For instance, a tannic acid concentration of 0.13 g/l, applied on the tongue of *Microcebus murinus* elicits a weak signal on the corda tympani proper nerve, while the lowest behavioural response is observed for 0.19 g/l (Hellekant *et al*., 1993; Iaconelli and Simmen, 1999). Accordingly, the two-bottle test is reliable method to estimate taste thresholds.

The supra-threshold responses are recorded with similar protocols: the profile of supra-threshold responses is determined by plotting the amount of solution ingested against concentration. The resulting profiles may resembled an unsymmetrical bell-shaped curve in the case of responses to sugar (in this case linear regression models are applied on the increasing part of the profile and on the decreasing part, after transforming data into their decimal logarithms), or tend towards an asymptote for the inhibitory responses to tannins.

To categorise the taste qualities perceived by a primate, another type of behavioural method is required, based on conditioning. For instance, conditioned taste aversion towards sugars is obtained by injecting lithium chloride into the abdominal cavity, immediately after the animal consumed a sweet solution. The nausea provoked by lithium chloride is associated to the taste after one trial, and the animal will avoid any sweet-tasting compound in next choice tests. In this case the notion of "sweet" actually refers to human perception and the corresponding semantic descriptor. In the case of a primate, such as *Microcebus,* the animal will react negatively to any substance the taste of which resembles that of the conditioned stimulus. This method has been used to determine, within a panel of substances tasting sweet to humans, which ones were also perceived as "sweet" by the primate (Hellekant *et al*., 1993).

Taste thresholds in human populations

In the research field of nutritional anthropology, a proper selection of the method for assessing taste abilities is paramount. The method for determining perception thresholds has been widely used in early studies of taste in humans. This method has many variants but generally involves two phases of testing.

An approximate detection threshold is first measured by providing various concentrations of a given compound, following an ascending or descending order (e.g. Harris and Kalmus 1949, Dixon and Massey 1969), and asking subjects whether they perceive a taste sensation different from that of water. A complementary test is then designed to check whether subjects are able to discriminate between water and solutions containing the concentration corresponding to this detection threshold. In this last phase, subjects are informed of the taste quality that they are supposed to discriminate from water. This method, which only involves discrimination against pure water, without recognition, has often been used to determine detection threshold in singlecompound studies.

An alternative procedure, however, is more relevant to the topics of nutritional anthropology which address the issue of taste as a determinant of food intake. Food selection necessarily involves recognition of taste stimuli elicited by foods in the oral cavity. In this respect, taste recognition thresholds have to be assessed. The method differs from that mentioned above because a set of compounds is generally tested rather than a single substance, and, more important, because subjects must recognise taste qualities of the various substances. Accordingly this reduces the influence of random responses.

The procedure (Hladik et al., 1986) is derived from the staircase method described by Cornsweet (1962): after informing the subject on the taste categories he or she could be faced with such as water, salty, sour, sweet, bitter, astringent, recognition thresholds are measured during a blind test (the order of presentation of compounds is not known by subjects). Solutions of tastants are presented in a semi-randomised order (Figure1), starting with the weakest solution in order of equally increasing concentration (i.e. 0.25 or 0.3 log increment). Substances like astringent tannins, the perception of which is likely to persist for a long period and might affect the sensitivity toward other substances, are generally given as the last stimuli within the set of compounds tested. Once the taste of two successive concentrations is recognised successfully, the subject is given the previous unrecognised solution (first reversal). This up-and-down procedure is performed twice until the taste of two increasing stimuli is correctly named. The actual recognition threshold is calculated as the arithmetic mean of the lowest concentrations recognised in each reversal.

Figure 1. Blind tests for determining taste recognition thresholds (Photo F. Aubaile)

This procedure provides a conservative estimate of recognition threshold. Other up-and-down procedures provide probabilistic figures, in which incorrect responses and correct responses allow the calculation of threshold (Dixon & Massey, 1969).

Under laboratory controlled situation, the use of de-ionised or poorly mineralised water to prepare the solutions has been recommended. However, under field conditions, it is often more realistic to use local drinking water as subjects are used to the peculiar taste of their own water sources. The powders for each product should be weighed precisely and, for research in the field, it is a good idea to take ready-measured and labelled packets. As an example, for a test with a series of solutions at twofold steps of increasing concentration, each series is created starting with the highest concentration; each sample is diluted in a beaker with 100 ml of water, using a magnetic agitator. A volume of 50 ml of this solution is then poured into the first numbered flask and the remainder is diluted again with 50 ml of water and so on until a series of flasks is created. The resulting dilutions for a selection of taste tests are shown below (Table 7.1).

Table 7.1. **A selection of appropriate taste test solutions (twofold steps)**

For fructose: 11 dilutions from 1 to 1,000 millimoles per litre.

For sucrose: 9 dilutions from 1.5 to 400 millimoles per litre.

For sodium chloride: 10 dilutions from 0.5 to 250 millimoles per litre.

For citric acid: 8 dilutions from 0.2 to 25 millimoles per litre.

For quinine hydrochloride: 11 dilutions from 0.4 to 400 micromoles per litre.

For tannic acid: 12 dilutions from 4 to 8,000 micromoles per litre.

For oak tannin: 10 dilutions from 0.023 to 12 grams per litre.

For 6-n-propylthiouracil (PROP): 12 solutions from 1.9 to 3,800 micromoles per litre.

A one-minute interval after water rinses is necessary before presenting further solutions. Rinsing the tongue with the same water as is used for the dilutions allows subjects to remain in contact with a reference solution before assessing the taste of proposed stimuli. At the group/population level, the median threshold can be calculated using probit analysis (Finney 1971) after clustering individual thresholds into discrete classes of concentrations. The use of median thresholds rather than mean thresholds is appropriate for some compounds like the bitter tasting 6-n-propylthiouracil (PROP), the perception of which follows a bimodal distribution (see below).

A third parameter that has been used in sensory psychophysiology studies is taste discrimination threshold. This measures the ability of subjects to discriminate the smallest variation of concentration from a reference solution (Weber ratio). Following the method of constant stimuli described in Galanter (1962), subjects are provided with pairs of stimuli, of which one is the reference concentration. Subjects are asked to say which of the two stimuli is the strongest. Pairs may be delivered in ascending order (Laing et al., 1993), or by selecting four increments below and four increments above the reference concentration with equidistant steps (Johansson et al., 1973). Within each pair, solutions are presented in a randomised order. Several reference concentrations can be used as discrimination thresholds vary with the level of concentration. By convention, the threshold or 'just noticeable difference' is determined as the concentration variation that is perceived by 50% of the individuals.

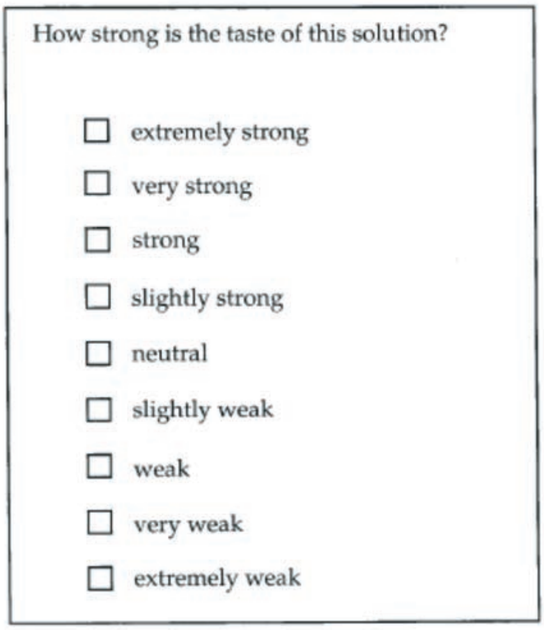
Measuring taste perception at a supra-threshold level

Apart from threshold measurements, it is particularly useful to characterise taste perception in terms of supra-threshold responses to stimuli. At this level one have to distinguish between the intensity of the taste quality perceived and the affective value associated with that taste. The perception of taste intensity, like for thresholds, is globally less dependent upon affective and cognitive factors than the hedonic value of gustatory stimuli.

There are many variants in the methods used to assess taste intensity, which are based on the use of scales. Typically, subjects indicate the intensity perceived when tasting a compound in solution on labelled scales or magnitude scales. As for other sensory measurements, the presentation of stimuli follows a random order or an increasing or decreasing concentration order. At least two trials of the same series are performed.

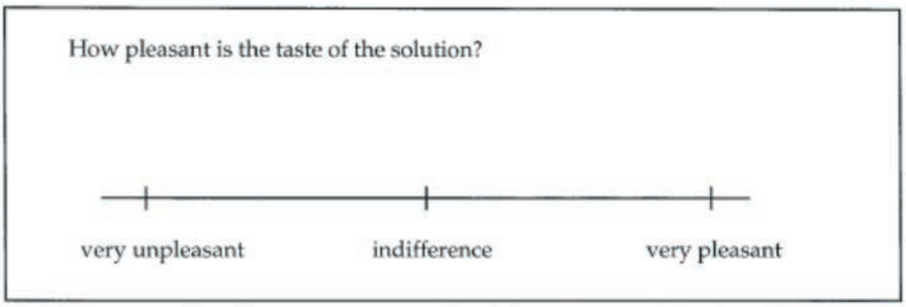
As for labelled scales, a 5-point scale was originally introduced by Likert (1932), but it is now more common to use 9- or even 11-point scales, displayed vertically or horizontally (Figure 7.2). Responses are converted to scores on a scale ranging, for instance, from 1 (extremely weak) to 9 (extremely strong). The mean of individual scores is taken to provide an overall population score.

Figure 7.2 Example of a vertical 9-point labelled scale



Another scale designed to rate taste intensities, utilising descriptive words, is a semantically labelled scale of sensation magnitude (LMS) (Green et al. 1993). Unlike previous scales, the scale is continuous and avoids ceiling effects (e.g. responses to concentrated stimuli tend to aggregate towards the top anchor of the scale). It also represents an absolute scale of perceived intensity while taking into account subject-specific intensity magnitude estimates. This scale is composed of six verbal semantic descriptors from barely detectable to strongest imaginable taste according to the geometric means of their rated magnitudes (Figure 7.3).

Figure 7.4 Visual analogues scale for hedonic rating

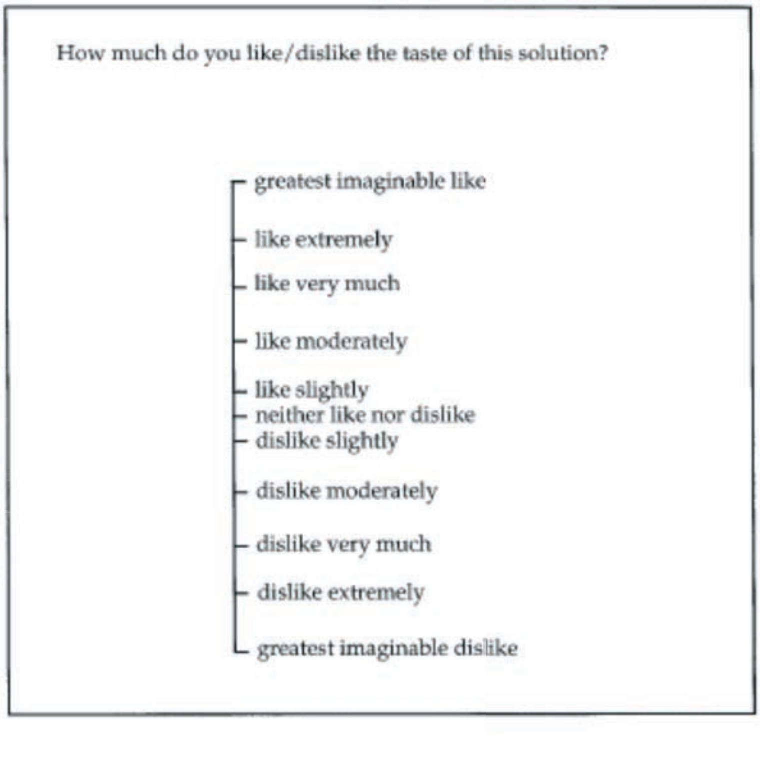


Taste hedonics is investigated using either labelled or visual analog scales. When using analog scales, the pleasantness or the unpleasantness of the sensation for a given stimulus is expressed by the subject, with a stroke on a line anchored with “maximal pleasure” at one end and “maximal displeasure” at the other end. In some cases, a sign indicating “Indifference” is displayed in the middle of the line. Also, subjects are allowed to express extreme responses beyond the visual limits of the scale. This occurs, for instance when a stimulus is judged more pleasant or more unpleasant compared with a concentration previously evaluated as eliciting maximal displeasure or pleasure (Figure 4). This hedonic or affective response is then translated into numeric values by measuring the distance (in mm) between the stroke and the neutral line. Positive values represent pleasant sensations and negative values unpleasant ones.

Visual analogue scales offer possibilities to assess taste hedonics in populations including non-literate informants or school children. An alternative is to use a faces scale in which a 7-point scale is replaced by stylised faces figuring expressions from joy to gloom (Andrews & Withey, 1976). Subjects are then asked to say which face is the closest to what they presently feel when tasting a solution. Stylised faces may be limited to represent only the extremities of the scale (‘grimacing face with tongue protruding’ at the left hand and ‘happy face licking its lips’ at the other end), which correspond respectively to the term ‘not liked at all’ and ‘liked a lot’ (Looy & Weingarten, 1992).

Scales labelled with varying numbers of points are often used to assess hedonic responses (e.g. Peryam and Pilgrim 1957). However, using this type of scale may be hampered by the ceiling effects, which, as is the case for taste intensity, reduce the discrimination among the most liked or disliked foods. The Labelled Affective Magnitude (LAM) scale, proposed by Schutz and Cardello (2001) allows one to circumvent this effect and to distinguish subgroups (Pasquet et al., 2002). This scale is an 11-point vertical scale with greatest imaginable pleasure and greatest imaginable displeasure at each end (Figure 7.5). The response (a bar on the scale) is measured positively, or negatively, from midway, to be re-scaled from –100 to +100 between the two extreme semantic labels (see also Macbeth and Mowatt, this volume).

Figure 7.5 Labelled Affective Magnitude (LAM) scale (after Schutz and Cardello 2001)



Another technique has been developed to investigate neonate taste responses or as an alternative to the use of hedonic scales. Such technique is based on the evidence that humans as well as non human primates display a gusto-facial reflex when in contact with concentrated taste stimuli. The video recording of such behaviour, which occurs rapidly after the stimulus is presented, allows to circumvent possible cognitive or culturally determined attitude which may arise when subjects are asked to judge solutions. In this method, facial expressions in response to the application of a taste stimulus on the tongue are recorded using a video tape. This method has been used in early studies of taste in non-human primates, including babies, and human neonates (Steiner, 1977; Steiner & Glaser, 1984). More recently, it has been applied to categorise mimics expressed by young adults in response to sweet substances (Looy & Weingarten, 1992). In this test, a panel of adults is asked to decide from videotapes figuring subject responses to taste stimuli, whether subjects like, are neutral or dislike the solution proposed. They indicate on a 5-point scale how confident they feel about their judgement.

A screening method applied to the investigation of perception of PTC/PROP substances

The genetically determined perception of PROP (6-*n*-Propylthiouracil) and PTC (Phenylthiocarbamide)-related bitter substances has received considerable attention in anthropological and sensory physiology literature. Early studies used the bimodal distribution of sensitivity (taster vs. non-tasters) in populations as a marker to study human genetic diversity (see review in Hladik & Pasquet, 1999).

More recently, investigations on PROP/PTC tasting aimed at understanding the relationship between genetically determined taste sensitivity and the development of taste preferences and food use (Drewnowski & Rock, 1995). For such studies, Bartoshuk (1993) used a three-group typology according to PROP sensitivity (respectively non-tasters, tasters and a group of highly sensitive individuals, the super-tasters). These groups are distinguished according to PROP detection thresholds within a range of 15 PROP solutions ($1.0\ 10^{-6}$ - $3.2\ 10^{-3}$ M) incremented in quarter-log steps. After separating tasters and non-tasters (cut-point at $2.0\ 10^{-4}$ M), the super tasters are then distinguished among tasters on the basis of the mean ratio of intensity of supra-threshold intensity rating PROP solutions relative to sodium chloride solutions.

A rapid and simplified screening method has been developed by Drewnowski et al. (1997) to avoid such a long testing process in population-based studies: the subjects are asked to place PROP-impregnated filter paper (dried after impregnation with a saturated PROP solution) on the back of the tongue, let it get moist and rate the bitterness on a nine-point category scale (from 1='not at all bitter' to 9='extremely bitter'). The subjects are then divided into three groups, respectively those who rated the paper 1 or 2, those who rated 3-7, and those who rated 8 or 9. A cross-validation (Monneuse et al., 2000) showed that the simplified method of Drewnowski et al. yielded results quite comparable to those obtained with the series of PROP solutions, thus permitting to discriminate 'non-tasters', 'tasters', and 'super-tasters'.

Conclusion

Methods for assessing taste perception in both non-human primates and humans are provided in this paper as anthropologists interested in the evolution of sensory systems and related literature need to be aware of methodological differences and associated terms. In particular, thresholds can be measured with different techniques and do not necessarily integrate similar meanings in sensory studies in humans and primates.

The issues addressed are crucial to choose among techniques. For instance in both non-human primates and humans, detection thresholds can be measured using a conditioned taste procedure in the first case and recording verbal responses to tasting solutions (blind test) in the second case. The resulting thresholds may be compared, especially if the aim of the study is to relate food selection to taste sensitivity.

In practice one should be cautious that subjects undergo sensory fatigability which imposes limitations to the number of tests that can be performed. For instance when determining recognition thresholds, a number of five or six different compounds is a maximum recommended to be investigated. Another aspect that must be borne in mind is the fact that trained subjects show better performances than naive subjects when tasting solutions (Pangborn, 1959). Accordingly, repeated measures may yield different values. This phenomenon however is reduced when tests are based on recognition of taste qualities instead of measuring 'just-noticeable differences' or taste detection thresholds.

Technically, one should be aware that the gustatory parameters measured are sensitive to sampling bias and variability, especially parameters involving hedonic aspects. It is thus recommended to carry out tests on relatively homogenous groups, differentiated either by sex, age classes, smoker/non smokers, pathologies, hormonal status, hunger state and other satiety factors (e.g. Bourlière et al., 1958; Whissell-Buechy, 1990; Bartoshuk et al., 1996; Bartoshuk, 2000). Anyone has already experienced the lowered perception of food taste during rhinitis (an effect which actually largely applies to the smell component of the oral sensation instead of taste perception). Regarding methods aimed at measuring taste intensities or hedonics, one should be cautious that scales, especially those which include verbal descriptors, may not necessarily be universally suited for cross-cultural comparisons and across age categories.

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