



Human Palaeontology and Prehistory

The evolution of taste perception: psychophysics and taste nerves tell the same story in human and non-human primates

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Abstract

This paper presents a parallel analysis of the results of recent studies of taste responses of humans and phylogenetically different non-human primates, in order to provide evidence of the evolutionary history of taste perception, and to discuss its present significance. A cluster analysis of the signals recorded on isolated nerve fibres of the various non-human primates shows additive trees representations, corresponding to a two-way system that allows discriminating what is beneficial from what could be toxic or anti-nutrient (sugars vs. alkaloids and tannins) among a large number of chemical stimuli. In humans, using psychophysical data (recognition taste thresholds) with a similar method of analysis, we observed the same dichotomy in the additive tree and similar covariation between some tastes thresholds, notably those of alkaloids and tannins. The converging results obtained by both methods show that the target of evolutionary pressure was a set of taste receptors that were not initially tuned to respond to what is presently described as basic tastes. *To cite this article: C.-M. Hladik et al., C. R. Palevol 2 (2003).* © 2003 Académie des sciences. Published by Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

L'évolution de la perception gustative : les données psychophysiques et les réponses des nerfs de la gustation correspondent à la même histoire évolutive de l'homme et des primates non humains. Une même méthode d'analyse des corrélations par les arbres additifs a été utilisée afin de comparer, dans une perspective d'étude de l'évolution de la perception gustative, les co-variations des réponses électrophysiologiques obtenues avec des primates non humains éloignés phylogénétiquement et celles obtenues par l'approche psychophysique sur des échantillons de populations humaines. Les signaux enregistrés sur les fibres du nerf gustatif des différentes espèces de primates non humains sont corrélés selon un arbre additif, qui présente une double ramification : d'une part, les signaux correspondant aux substances bénéfiques (des sucres), d'autre part, les signaux provoqués par des substances susceptibles d'être défavorables, par effet toxique ou anti-nutritif (des tannins et des alcaloïdes), ces deux ensembles se distinguant clairement de tous les autres stimuli gustatifs. Chez l'homme, on retrouve la même dichotomie à partir des corrélations entre les seuils de reconnaissance avec, en particulier, une corrélation entre la

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perception des tannins et celle des alcaloïdes. La convergence des résultats obtenus par ces deux approches montre que les pressions de sélection ont favorisé l'émergence d'ensembles de récepteurs, qui ne correspondent pas forcément aux « saveurs de base » classiquement décrites en psychophysiologie. *Pour citer cet article : C.-M. Hladik et al., C. R. Palevol 2 (2003).*

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Version française abrégée

Pour comprendre la signification adaptative du système gustatif des primates, incluant l'homme, nous avons utilisé une même méthode d'analyse des corrélations par les arbres additifs, sur les co-variations des réponses gustatives. Celles-ci ont été mesurées, chez des primates non humains phylogénétiquement éloignés (*Callithrix jacchus*, Callitrichidae ; *Macaca mulatta*, Cercopithecidae ; *Pan troglodytes*, Pongidae), par le biais des fréquences des impulsions sur les fibres isolées du nerf de la gustation en réponse à des solutions appliquées sur la langue. Chez l'humain, les seuils de reconnaissance gustative pour différents produits, déterminés en simple aveugle sur des échantillons de populations (412 sujets adultes), ont été utilisés d'une manière analogique. Les résultats obtenus avec les mêmes produits solubles (fructose, saccharose, acide citrique, chlorure de sodium, quinine, tannin de chêne, acide tannique) montrent que les corrélations entre les réponses pour ces différentes substances sont très comparables d'une espèce à l'autre, en dépit de la spécificité des méthodes utilisées dans chacune des deux approches. Chez tous les primates étudiés, incluant l'homme, les corrélations significatives entre les perceptions du goût amer de la quinine et du goût des tannins (un goût astringent qui est plus qu'un simple phénomène tactile) indiquent que plusieurs récepteurs périphériques sont communs à chacune de ces perceptions. Sur les arbres additifs, l'importance de la distance entre l'ensemble des tannins + quinine et celui des sucres indique que, parmi les transducteurs gustatifs mis en jeu pour chacun de ces groupes de substances, il n'y a pas (ou que très peu) de récepteurs communs. Dans tous les cas, la corrélation négative entre ces deux ensembles de signaux, correspondant respectivement à des substances bénéfiques (les sucres, source d'énergie) et à des produits que les primates

doivent éviter (à effet toxique, comme beaucoup d'alcaloïdes, ou anti-nutriments, comme les tannins), montre qu'il n'y a pas de récepteurs périphériques communs à ces deux ensembles de réponses gustatives. Cette dichotomie apparaît comme le résultat de la co-évolution des primates et des angiospermes, dont les fruits sucrés permettent la dissémination des graines, mais dont les teneurs en produits secondaires (alcaloïdes, tannins, terpènes, etc.) nécessitent une détection rapide et leur évitement. L'appareil gustatif des primates permet de détecter de nombreuses autres substances, en particulier le chlorure de sodium. Cependant, dans ce contexte, le goût salé, tel qu'il est perçu et décrit par l'Homme, peut difficilement être mis en relation avec la co-évolution avec des aliments potentiels des milieux naturels, où les concentrations en chlorure de sodium sont généralement inférieures au seuil de détection. La détection des solutions concentrées de chlorure de sodium, comme dans le cas de substances non présentes dans le milieu naturel tels les PTC ou PROP (perçus comme amers par certains « goûteurs »), témoigne de la diversité de récepteurs gustatifs dans un système permettant aux primates une grande adaptabilité, en relation avec la diversité des produits de l'environnement. Mais cette diversité des perceptions (qui n'est pas limitée aux quatre « saveurs de base ») se structure selon une dichotomie permettant la discrimination rapide des substances énergétiques et des produits potentiellement toxiques ou anti-nutritifs.

1. Introduction

During the Cainozoic, when plants bearing fleshy fruits expanded, selective pressure would have been exerted on the primate tasting system to enable the various species to perceive and identify either beneficial or toxic constituents of the foods available in

changing environments [12]. To maximise ingestion of beneficial substances, gene(s) would have been selected to promote a set of taste receptors triggering a positive response towards sugars. Similarly, a selective pressure would have led to the development of adequate avoidance responses to compounds likely to be toxic and/or antinutrient, the most common being alkaloids and tannins. In this paper, we present a parallel analysis of the results of recent studies of taste responses of humans and non-human primates, in order to provide evidence of such selective pressure, and to discuss the significance of present taste perception.

2. Methods

In humans, data on recognition thresholds were obtained during blind tests using verbal recognition of tastes with solutions (including fructose, sucrose, sodium chloride, citric acid, tannic acid, oak tannin and quinine hydrochloride) at increasing concentrations, in a stepwise fashion [10, 11].

In anaesthetised marmoset (*Callithrix jacchus*), rhesus monkey (*Macaca mulatta*) and chimpanzee (*Pan troglodytes*), the number of impulses per second was recorded from single nerve taste fibres, while their tongues were stimulated with solutions at above-threshold concentrations [2, 5–8].

We selected here, among data obtained in several of our published or unpublished studies, those concerning compounds used for both non-human primates and humans, to show, for each species, similarities/dissimilarities of responses between the compounds used as stimuli. Each set of data was subjected to additive trees clustering [16] for modelling similarity/dissimilarity data, using SYSTAT (version 9.0) statistical software (SPSS Inc., Chicago). The radial representation of the trees (not provided by SYSTAT) was drawn using the T-Rex Program (freely available at www.fas.umontreal.ca/BIOL/Casgrain/en/labo/trex/index.html).

3. Results

Additive trees are presented in Figs. 1 and 2. Stress indices of each tree are low (< 5 %), thus indicating a good representation of the data concerning 412 human subjects (Fig. 1), and, for each species of non-human

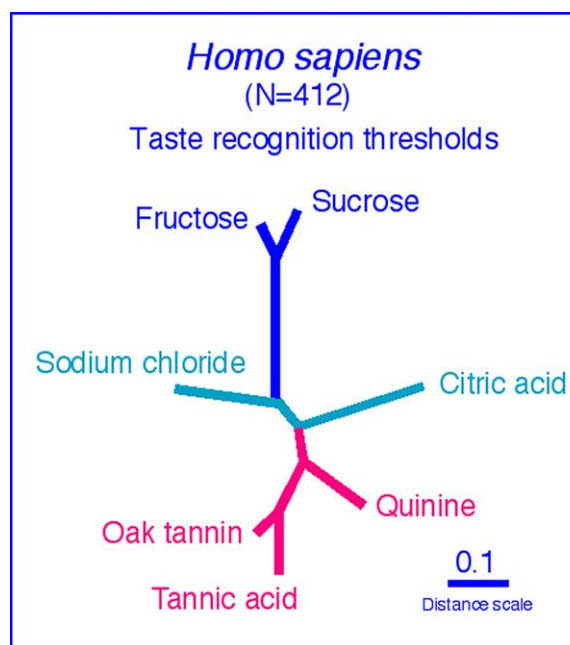
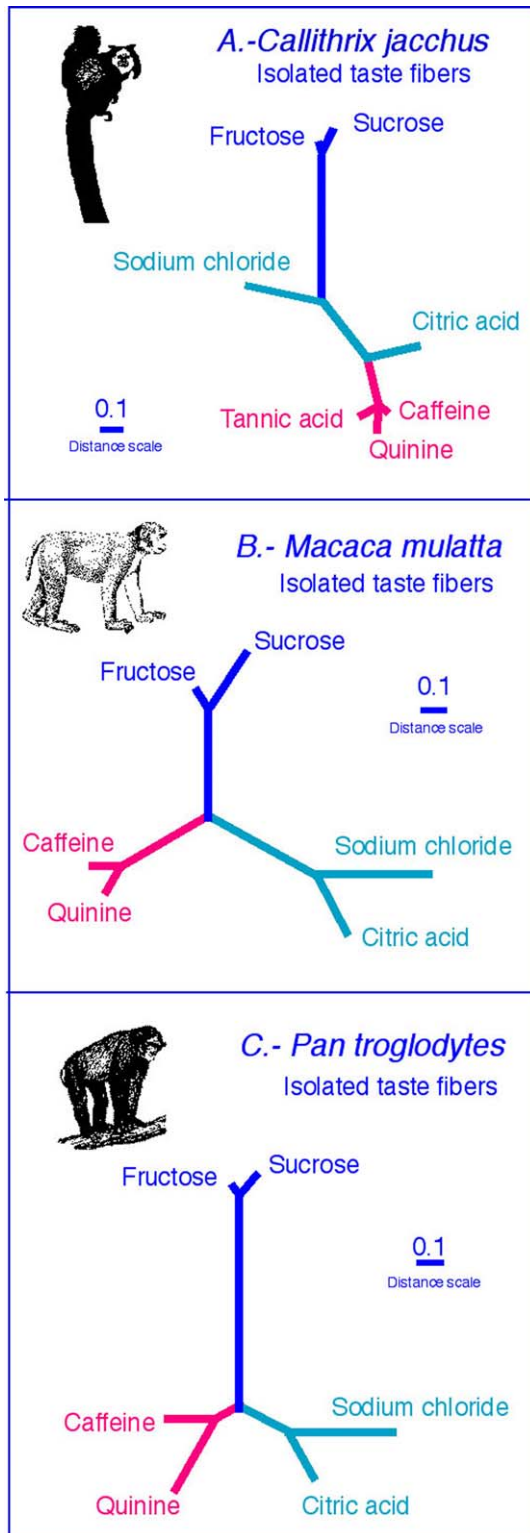


Fig. 1. Additive tree (stress = 2.5%) showing relationships between taste recognition thresholds for 412 human subjects.

Fig. 1. Représentation radiale (arbre additif) de la matrice des distances calculées à partir des corrélations entre le seuil de reconnaissance de différentes substances chez 412 sujets humains adultes. La distance traduit les ressemblances/dissimilitudes des perceptions. La valeur du stress (2,5 %) témoigne de la bonne qualité de la représentation arborée par rapport aux données recueillies.

primates (Fig. 2), about 50 isolated taste fibres. Results obtained from studies of humans and non-human primates appear remarkably similar with regard to the relationships between taste perception of different compounds, although the methods used for recording taste responses in the different studies were very specific.

The human data (Fig. 1) show that, if an individual has a high sensitivity to sucrose, he/she will also show a high sensitivity to fructose. Although co-variation is a clear indication that most receptors involved in sucrose perception are also involved in tasting fructose, the moderate correlation level obtained suggests that various sugars may not elicit exactly the same taste signal. More striking is the correlation between perceptions concerning quinine and the two tannins (tannic acid and oak tannin), shown by relatively short distances in the additive tree. The bitter taste of several alkaloids obviously differs from the astringency of most tannins (whose peculiar taste [18] is not a mere



tactile perception due to precipitation of salivary protein). Again, the co-variations found in this alkaloid/tannin cluster might reflect the responses of partially overlapping sets of taste receptors. Covariation in individuals' sensitivities to bitter compounds was also presented by Delwiche et al. [3] as an evidence supporting multiple receptor/transduction mechanisms. Furthermore, our data show that sensitivity to sucrose or fructose varies independently of sensitivity to quinine and tannins. Hence, no significant set of taste receptors responds to both sugars and alkaloid/tannin.

The non-human primate taste fibre data (Fig. 2) allows a further step in understanding the functioning of the peripheral taste system. In the three species, individual taste fibres highly responsive to sucrose are also responsive to fructose. As for human taste thresholds, distances between these carbohydrates are short in the additive trees. However, correlations vary to some extent among primate species. For instance, in the rhesus monkey, *Macaca mulatta* (Fig. 2B), fructose and sucrose may be partly discriminated at a peripheral level [7].

In the three non-human primates investigated, there is also a clear relationship between responses to quinine and tannic acid (when tested), and other compounds that taste bitter or astringent to humans, such as caffeine and aristolochic acid. One single taste fibre can be involved in the signalling of these various compounds (and, in some instances, of citric acid) [2, 5–7]. Furthermore, a high response to soluble sugars in an individual taste fibre involves a low response (or no reaction) to quinine, tannins, or to various other compounds, including salts and acids. These data point out

Fig. 2. Additive trees showing the relationships between taste signals recorded on isolated taste fibres in three non-human primate species, respectively for the marmoset, *Callithrix jacchus* (A; stress = 1.5%), the rhesus monkey, *Macaca mulatta* (B; stress = 5.0%), and the chimpanzee, *Pan troglodytes* (C; stress = 3.5%).

Fig. 2. Représentation radiale (arbre additif) de la matrice des distances calculées à partir des corrélations entre potentiels enregistrés sur des fibres isolées du nerf gustatif (*chorda tympani*) en déposant sur la langue du primate les différentes substances. La distance traduit les ressemblances/dissimilitudes des signaux. Les valeurs du stress, respectivement 1,5 %, 5,0 % et 3,5 % chez le ouistiti *Callithrix jacchus* (A), chez le macaque rhésus *Macaca mulatta* (B) et chez le chimpanzé *Pan troglodytes* (C), témoignent de la bonne qualité de la représentation arborée par rapport aux données recueillies.

a clear dichotomy, in non-human primates, between compounds likely to be toxic (perceived as bitter or astringent in humans) and compounds likely to be beneficial (perceived as sweet in humans).

4. Discussion

4.1. Behavioural and morphological dichotomy

In terms of primate feeding behaviour, the dichotomy in taste discrimination is reflected by a preference for sugars and a rejection of most alkaloids and tannins [2]. The gusto-facial reflex, observed in the newborn of various species, including *Homo sapiens* [19], highlights the innate nature of this dichotomy, allowing infants to swallow sugars and to spit out quinine. The reflex can be understood in light of the evolutionary history of the Primate Order. Selection pressure led to the co-evolution of the angiosperms producing fleshy fruits with increasing content of soluble sugars (fructose, sucrose and glucose) and frugivorous seed dispersers (birds and primates) with increasing taste sensitivity and preference for sugars [9]. The high energy needs in the largest species were met with the global trend (allometric relationship) towards highest sensitivity to fructose and sucrose [17]. Conversely, the occurrence of alkaloids, tannins, and various other more or less toxic compounds in plants should have co-evolved with the ability of primates (and other vertebrates) to taste what is presently described as bitter or astringent in the human repertoire.

Although several kinds of taste receptors may be responding to various compounds perceived as bitter, as shown by the number of putative G-protein-coupled receptors [13], the topological grouping of fibres responding to aversive substances and their cortical projection is a likely evolutionary step towards an efficient gusto-facial reflex.

Indeed, between the front and the back of the tongue, there seems to exist a major dichotomy between ‘bitter’ and ‘sweet’ in higher primates, as judged by taste nerve recordings from the rhesus monkey [7]. The front of the tongue is innervated by the chorda tympani nerve (CT), while the glossopharyngeal nerve (NG) mediates taste from the back, a morphological trait shared by mammals, including higher primates. Among single fibres from the CT and NG nerves of rhesus monkey, a majority responded to sugars in the

CT (16 out of 47 fibres versus only four responding to quinine), whereas the majority in the NG (20 out of 33 fibres) responded to quinine, as compared responding to sugars. Furthermore, the average response to sucrose in the fibres of the CT was 23.9 impulses per sec (SD 2.7) as compared to 11.3 impulses per sec (SD 2.3) in the few fibres of the NG responding to sugars. Thus, not only there are many more fibres eliciting a signal for sugars from the front of the tongue than from the back, but also they are more sensitive to the same stimulus.

4.2. Why are there so many taste responses?

Indeed, besides this global dichotomy, a large variety of taste responses can be observed. For instance, among bitter compounds, the well-known examples of PTC (phenylthiocarbamide) and PROP (6-*n*-propylthiouracil), involving various proportions of ‘tasters’ and ‘non-tasters’ in human populations [4], were considered to be the best way to understand taste genetics [1, 14] and food preference [15]. However, this factor, which has been tested in our studies on human thresholds [11], is independent of the sensitivity to other substances, including alkaloids/tannins.

Similarly, one may wonder why human taste thresholds for citric acid and sodium chloride co-vary poorly with thresholds for other compounds. Perception of acids might have been subjected to selective pressure for innate rejection, as for tannins/alkaloids. There is evidence that foods with a low pH are avoided by primate species when the symbiotic flora in their digestive tract could be strongly disturbed [21]. Observations on taste fibres of the marmoset, *Callithrix jacchus* (Fig. 2A), showing that a group responding to citric acid is not clearly separated from the set responding to tannin/alkaloids, is part of the evidence. However, this type of correlation is poor or absent in the rhesus monkey, *Macaca mulatta* (Fig. 2B) and in the chimpanzee, *Pan troglodytes* (Fig. 2C).

Another issue is raised by sodium chloride, which (at a relatively high concentration) elicits a clear signal in taste fibres, though it is present at undetectable concentrations in the natural foods of most extant primate species [10]. Among the fibres responding to sodium chloride in the chimpanzee, some also respond to KCl, others to monosodium glutamate (MSG), and some to KCl and MSG [5, 6]. Their response, in the rhesus monkey, is restricted to salts, but excludes

KCl [7]. Mixtures of salts might be target of selective pressure; however, since it is so important to monitor and maintain adequate levels of Na, we may wonder why primate taste thresholds are not adapted to detecting NaCl in the foodstuff of the natural environment. The answer probably lies in the complementary mechanisms that are involved in feeding behaviour [20], allowing the intake of foodstuffs containing micronutrients at undetectable concentration levels. For such compounds, positive conditioned responses to the beneficent effect of micronutrient can be mediated by sensory cues different from specific tastes of the micronutrients.

4.3. Taste as a target of evolutionary pressure

Our data, on phylogenetically different primate species, show that the target of evolutionary pressure is a set of chemical receptors that was probably not initially tuned for sweet, bitter, sour, or salty tastes, thus allowing a large flexibility in the long-term evolutionary response to variation in plant composition. The set of receptors best responding to soluble sugars of the fruits of the angiosperms have been retained mostly in the front part of the primate tongue, with the corresponding nerve fibres connected to primary taste areas of the brain stem eliciting a positive gusto-facial reflex [19]. The set of receptors best responding to alkaloids and tannins, or strong acids (eventually also to other secondary compounds not yet studied for taste, such as saponins and terpenes) have been selectively retained on the rear part of the tongue, and connected to the part of the brain stem eliciting a negative gusto-facial reflex. Taste receptors diversity still allows responses to substances that are uncommon or present at low concentration in the natural habitat of the primates. If such compounds are present at detectable concentration, the taste signal can elicit a conditioned (positive or negative) response. It possibly occurred with the invention of cooking by Middle-Pleistocene members of the genus *Homo* [22], when they started to add salt to improve the taste of cooked foods, even though salty taste was not initially positively or negatively selected in wild primate taste responses.

Since our data from marmosets, rhesus monkeys, and chimpanzees reflect adaptations to discriminate, among a wide array of tasting compounds, what is beneficial from what is to be avoided, the additive tree

concerning human taste thresholds, by virtue of its similarity with that of non-human primates, also reflects the evolutionary history of our tasting system.

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