



## Review

## The avian taste system: Potential implications in poultry nutrition

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## ABSTRACT

Taste has evolved largely as a mechanism to identify nutritious foods and is important for detecting nutritionally relevant carbohydrates, amino acids, lipids, salts and toxic compounds. Species differences in the taste system are intimately related to ecological niche and food availability. It has been argued that birds have a lower taste acuity compared to mammals due to their low taste bud numbers. In addition, chickens seem to have fewer taste receptor genes: the sweet taste receptor is missing and their bitter taste receptor repertoire is very small, consisting of only three members. Furthermore, chickens compared to pigs show a lower sensitivity to glucosinolates. However, chickens are able to quickly adapt their feeding behaviour based on taste cues and the ratio of the number of taste buds/oral cavity volume is higher than in most mammals. Compared to ruminants, chickens show higher aversion to glucosinolates and compared to humans a similar avoidance to quinine chloride. Moreover, many birds (including commercial chicken breeds) seem to have high acuity for dietary calcium. Emerging knowledge mostly derived from genome sequencing, shows that birds have a well-developed taste system. Predicted taste genes for umami, sour, salt, bitter, calcium and lipids are present in the chicken, turkey and zebra finch genomes. Preliminary data indicate that the umami taste receptor may be intact in chickens and that the bitter taste receptor repertoire is small in chickens, but in some bird species it is as large as in mammals. Some of the novel findings outlined in the review have the potential to bring important innovations to the practice of poultry nutrition such as reduction in phosphorus excretion, optimize the use of amino acids and fats, use of alternative feed-stuffs or the short and long term manipulation of feed intake. In conclusion, the avian taste system is well developed but differs significantly with different species. Behavioural and genetic evidence show that birds have an accurate capacity to detect different taste modalities challenging the broad consensus that birds have lower taste acuity than mammals. Finally, avian taste is intimately related to nutrient sensing and, consequently, to poultry nutrition practices.

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**Abbreviations:** AA, amino acids; BLAST, basic alignment search tool; Ca, calcium; CaSR, calcium sensing receptor; ENaC, epithelial amiloride-sensitive sodium channel; GIT, gastrointestinal tract; GLU, glutamic acid; GLUT2, glucose transporter 2; Na, sodium; NaCl, sodium chloride; PepT1, peptide transporter 1; P, phosphorus; SGLT1, sodium-glucose co-transporter 1; TR, taste receptors; T1R(1,2,3), taste receptor family 1 proteins 1 2 or 3; T2R, taste receptor family 2; TSC, taste sensory cell.

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## 1. Introduction

Taste genes show one of the strongest signatures of positive selection in vertebrates, suggesting that taste can play a critical role in the survival and adaptation of a species (Shi and Zhang, 2006; Kosiol et al., 2008). Most differences between taste systems of vertebrate species are related to their adaptation to dietary regimes (Jiang et al., 2012a). The peripheral taste system functions as a network of nutrient sensors that uncovers the nutritional value of foods. The direct relationship between taste and nutrition is supported primarily by the evidence that all the main natural taste agonists known are nutrients or anti-nutritional factors. For example, sweet taste is related to digestible dietary carbohydrates, such as mono and disaccharide sugars. Umami taste is related to dietary protein and senses some L-amino acids (AA), such as glutamic acid (Glu). Bitter taste detects potentially toxic molecules present in the diet. Salt and sour tastes are triggered by sodium (Na) and acids (H<sup>+</sup>), respectively. In addition to the classical primary tastes, fat, calcium (Ca), complex carbohydrates and water may also be perceived through taste mechanisms (Bachmanov and Beauchamp, 2007; Tordoff et al., 2008).

Over the last decade, the genomic information available through online gene databases has increased exponentially together with novel molecular biology and bioinformatic tools. There are currently three bird genomes available: the chicken or red jungle fowl (*Gallus gallus domesticus*), the turkey (*Meleagris gallopavo*) and the zebra finch (*Taeniopygia guttata*). This review deals with the genetic data relevant to the topic of taste in poultry. Since the discovery of the first taste receptors (TR) over a decade ago (Hoon et al., 1999; Matsunami et al., 2000), the field of taste biology has experienced a dramatic increase in research activity. Among other relevant findings, a full repertoire of TR has been well characterized uncovering new primary taste candidates such as for fats (Cartoni et al., 2010). In addition, the taste system has been described outside the oral cavity in several mammalian species including some farm animals such as the pig (Roura, 2011). The taste machinery in non-taste tissues seems to constitute a diffuse chemosensory system that monitors the nutritional status of the animal (Ren et al., 2009). This could have important practical implications in farm animals. However, a comprehensive review on what is known in avian species is lacking.

This review will first give a brief overview of the taste system in mammalian species as an introduction to a detailed review on our current understanding of the avian taste system that emphasizes potential applications in poultry nutrition.

## 2. The mammalian taste system

The taste buds are epithelial structures present in the oral cavity that consist of clusters of circa 100 taste sensory cells (TSC). In mammals the taste buds are grouped in papillae located on the tongue and throughout the oral cavity. A general tendency across mammalian species is that the number of taste buds seems positively correlated with the size of the mouth. For example, ordered in increasing volume of the oral cavity, hamster, rat, cat, human and pig have 723, 1438, 2755, 7902 and 19,904 taste buds respectively (Travers and Nicklas, 1990; Roura et al., 2008). Each bud is composed of at least three different functional TSC types: type I for sensing sour, type II for sensing sweet, umami and bitter and type III for transferring the signal to sensory neurons (DeFazio et al., 2006). The stimulation of TSC is mediated through TR. Some of the receptors belong to the super-family of G protein-coupled receptors and have been divided into two families: T1R and T2R. The T1R sub-family consists of three genes that form two heterodimeric receptors which sense umami (T1R1/T1R3) and sweet (T1R2/T1R3) (Li et al., 2002). The T2R is the bitter receptor sub-family consisting of around 20–40 genes in mammals studied to date (Shi and Zhang, 2006).

In addition to the oral cavity, nutrients and toxins present in food need to be monitored once they leave the mouth and travel further down into the digestive tract. In mammals, the chemosensing system may use the same sensors in the oral cavity and along the gastrointestinal tract (GIT) (Wellendorph et al., 2010). Nutrient-evoked GIT reflexes seem to be initiated by sensory cells located in the epithelia of the small intestine. In mammals, taste receptor proteins (e.g. T1R1, T1R3, T2R and  $\alpha$ -gustducin) are colocalized in enterocytes, Paneth cells, and solitary chemosensory cells (Sbarbati and Osculati, 2005). In addition, TSC have been located in stomach, colon and other digestive and non-digestive tissues (Treesukosol et al.,

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