Nutrient sensing, taste and feed intake in avian species

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Abstract

The anatomical structure and function of beaks, bills and tongue together with the mechanics of deglutition in birds have contributed to the development of a taste system denuded of macrostructures visible to the human naked eye. Studies in chickens and other birds have revealed that the avian taste system consists of taste buds not clustered in papillae and located mainly (60 %) in the upper palate hidden in the crevasses of the salivary ducts. That explains the long delay in the understanding of the avian taste system. However, recent studies reported 767 taste buds in the oral cavity of the chicken. Chickens appear to have an acute sense of taste allowing for the discrimination of dietary amino acids, fatty acids, sugars, quinine, Ca and salt among others. However, chickens and other birds have small repertoires of bitter taste receptors (T2R) and are missing the T1R2 (related to sweet taste in mammals). Thus, T1R2-independent mechanisms of glucose sensing might be particularly relevant in chickens. The chicken umami receptor (T1R1/T1R3) responds to amino acids such as alanine and serine (known to stimulate the umami receptor in rodents and fish). Recently, the avian nutrient chemosensory system has been found in the gastrointestinal tract and hypothalamus related to the enteroendocrine system which mediates the gut–brain dialogue relevant to the control of feed intake. Overall, the understanding of the avian taste system provides novel and robust tools to improve avian nutrition.

Key words: Chickens: Feed intake: Growth: Nutrient sensing: Regulatory genes: Taste

Introduction

Optimising the consumption of balanced diets is critical to the welfare, development, health and productivity of animals, particularly when raised or kept in captivity. In non-forced animal feeding scenarios, dietary choices are a result of the preference for available feeds or ingredients and the motivation to eat which, in turn, reflects the innate drive of preserving or achieving nutritional homeostasis[1]. The maintenance of the nutritional balance (or homeostasis) is a dynamic process that implies the existence of a network of nutrient sensors covering critical physiological functions. Thus, the term nutritional chemosensing was coined to describe studies on the sensing of nutrients in biological systems including the molecular mechanisms related to changes in genomic, metabolic, physiological and behavioural parameters[2]. In mammals and birds, dietary nutrients are perceived in the oral cavity mainly through the taste system which has evolved to differentiate nutrients from toxins[3,4]. Taste sensory cells form the taste buds in the oral cavity and translate nutrient sensing into neuronal signals (through cranial nerves) to the primary gustatory cortex of the brain. Chickens seem to have developed an acute sense of taste which enables them to distinguish at least five of the six primary tastes including fatty, umami, salty, sour and bitter (it is noted that the acceptance of fatty acid sensing as a differential taste type is still controversial particularly in chickens)[5,6]. In addition, the existence (or lack) of sweet taste linked to carbohydrate sensing in chickens remains unclear and will be further discussed in the 'Nutritional chemosensing in chickens: the molecular inside to taste' section[6–8].

Similar to mammals, birds integrate gustatory perception with post-ingestive events, particularly originating in the gastrointestinal system, to control feed intake[9]. In this context, extra-oral sensing of nutrients has been recently attracting a lot of attention, collating the importance of nutrient receptors (including taste receptors) and related downstream pathways on the control of feed intake[2,6,10–14]. The existence of this network of nutrient sensors outside the oral cavity implies that behavioural studies assessing the effect of taste in the control of feed intake need to be assessed with caution since pre- and post-ingestive nutrient sensing can be easily confounded. In the following sections, the present review will outline the main scientific findings covering oral and extra-oral nutrient sensing (but not always discerning which one of the two or both are the main drivers) relevant to chicken diet selection, feeding behaviour, oral/tongue anatomy, and nutritional genetics and genomics organised in a chronological order (Table 1).

The avian taste and nutrient-sensing system: research highlights

Table 1 represents a chronogram of the avian taste and feed intake research featuring the highlights of what has been

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Table 1. Chronological accountancy of the main peer-reviewed publications on taste and nutrient sensing and feed intake in poultry grouped by scientific discipline

Year	Main findings relevant to nutrient sensing, taste and feed intake	Behaviour	Physiology/ anatomy	Genetics/ genomics
1880	No taste buds found in birds[15]*		√	
1904	Taste buds were found in avian species[16]*		√	
1906	Taste bud distribution in birds found to be correlated with internal anatomy of the oropharynx. Four cell types described: neuroepithelial, supporting, peripheral and follicular[17]*; taste bud innervation consists of three neuronal nets: sub-gemmal, perigemmal and intra-gemmal[18]*		√	
1910	Taste buds found in the palate, oral-mandibular and dorsal–posterior tongue areas[19]*		√	
1946	Pigeons average thirty-seven taste buds, with about 71 % of them located on the dorsal tongue[130]		√	
1953	Feed choices for bobwhite quails rejecting Na, Ca, K, NH_4 and Li, but preferring sucrose over water[131]	√		
1957	Chickens preferred sucrose independent of energy and avoided saccharine relative to water[86]; taste sense in chickens is more rudimentary than that in humans[132]	√		
1959	Birds have TR in the posterior tongue and pharynx which respond similar to those of mammals[24]; fowls can discriminate between carbohydrates but sweetness perception differs from that in humans[87]; eight taste buds identified in 1-d-old chicks while twenty-four taste buds on the base of the tongue and floor of the pharynx in 3-month-old chicks[133]	√	√	
1960	Flavoured feed and water decreased intake in chickens[31]; feral pigeons shown to be responsive to many taste stimuli including sucrose but indifferent to glucose[134]	√		
1961	Preference of chickens can be reduced due to potential feed toxicity[135]	√		
1962	The tongue in chickens responds to low concentrations of FeCl and sucrose octa-acetate (bitter) and high (0·5 M) concentrations of sugars[83]; chickens and pigeons respond similarly to rats in NaCl solution preference[136]; chicks from 1 to 3 weeks change their preference from alkaline to mild acid solutions particularly from organic acids (relative to inorganic acids)[137]; bitter (quinine) conditioning to colour proved in chickens[138]	√	√	
1965	Japanese quails prefer sweet (10 % glucose) and sour (0·05 % HCl), reject salty (2 % NaCl) and bitter (1·25 % sucrose octa-acetate) solutions[84]	√		
1966	Negative preference for calcium lactate in Ca-deficient chicks suggested taste importance over nutritional requirements[60]	√		
1967	Jungle fowl prefer sucrose solution over water but not domestic chickens except when offered a low-energy diet[139]	√		
1969	Japanese quail preferred sucrose solution over water not related to energy but palatability[85]	√		
1971	Specific appetite for Ca is a learnt preference by which chickens can recognise Ca-deficient and -supplemented diets[61]	√		
1972	A 3-min test (pre-absorptive) showed preferences for 5 % sucrose and indifference/rejection for Na, K, CaCl, HCl, glucose and fructose solutions in chickens[32]	√		
1975	Lesions in the stratum cellulare externum of the brain of chickens inhibited gustatory stimulation by quinine solution (5 mM), suggesting a functional role in taste perception equivalent to the ventrobasal complex in the mammalian gustatory cortex[21]		√	
1976	Increased quinine acceptance after water deprivation, possibly due to changes in taste sensitivity in chickens[47]	√		
1977	Taste system found functional before hatching in chickens[140]	√		
1978	Laying hens decreased their feed intake when exposed to different Ca levels indicative of specific Ca appetite[56]; functional extra-lingual chemoreceptors found in chickens[141]; dietary choices in pullets based on protein intake (protein-specific appetite) related to physiological requirements[142]; dietary choices in chickens based on the protein:carbohydrate ratio to reach a similar growth than dietary balanced no-choice controls[143]	√		
1979	Broilers change supplemental Ca intake in response to changes in dietary Ca to match requirement[57]; tongue and beak movements related to sweet taste stimuli while beak wiping and head shaking related to stickiness, viscosity and irritation[144]	√		
1982	Heritability of taste acuity measured showing slow growers more sensitive to quinine and dextrose than fast growers[33]			√
1983	Chorda tympani nerve is key in chicken taste perception[145]; starling birds preferred 0·5 and 1 M concentrations of glucose and fructose and rejected sucrose relative to water[146]; chicken taste buds structure showed a longer canal leading to a pore via the superficial strata of epithelium compared with those of other vertebrates, even though both may have three similar cell types[147]; poultry can perceive dietary bitter compounds, with geese showing higher sensitivity than chickens, turkeys and Japanese quails[148]; taste cues potentiate chicks' aversion to salty feed[149]	√	√	
1984	Proof of specific appetite for Ca but low regulation of Ca intake in laying hens[150]	√	√	
1985	316 taste buds were found in 1-d-old chicks: 69 % on upper palate, 29 % on lower palate and 2 % on anterior tongue[26]		√	
1986	Chorda tympani innervates taste buds fundamental to maintain structural integrity[30]		√	
1987	Similar sequence of taste bud development in chickens and mammals[22]; chicks preferred a diet with excess AA (excess amount) to a control balanced feed in double-choice[49]	√	√	
1988	Red-winged blackbirds, common grackles and European starlings prefer a 1:1 mixture of glucose and fructose over water[151]	√	√	
1989	Broilers rejected saccharin-, citric acid-, salt- and quinine-flavoured to non-flavoured diets in two-choice tests[152]	√		
1990	In post-hatched chicks taste-driven avoidance seems to be more developed than attraction[82]; L-AA sensing cues are relevant to foraging decisions of red-winged blackbirds and starlings[153]	√		

Table 1 *Continued*

Year	Main findings relevant to nutrient sensing, taste and feed intake	Behaviour	Physiology/ anatomy	Genetics/ genomics
1992	European starlings showed higher avoidance to benzoate esters than alcohols while acidic groups reduced repellence[41]	√		
1993	The taste cell turnover rate in chickens is 4·5 d which is almost half of that in mammals[23]; the ability of broilers to adjust intake and/or select feeds to compensate for AA deficiencies depended on genetic stock and the type of AA[50,154]; chickens preferred long-chain TAG over MCT which increased plasma cholecystokinin[100]	√	√	
1996	Chickens showed taste-driven preferences for dietary oils[36]; supplementation of glutamic acid to a crude protein-deficient diet improved growth performance in chickens[51]; a (non-taste) post-ingestion mechanism reported to explain decreased feed intake due to excess dietary phenylalanine[155]; chickens preferred non-flavoured diets to diets flavoured with long-chain TAG or MCT[156]	√		
1997	Jojoba oilseed plant meal decreased feed intake of chickens presumably due to taste[46]; chickens responsive to taste- and/or odour-driven passive avoidance learning[157]; methyl anthranilate odour but not denatonium benzoate increased chicks' latency to drink or eat[158]	√		
1998	Pre-hatching experience of stimuli may affect the chicken's taste preference after hatch[159]	√		
2000	Mesenchymal cells found to be the precursors of taste bud cell development[73]; chickens did not show avoidance learning to denatonium benzoate[160]	√	√	
2001	Cockatiels discriminated between water and 0·16 M-KCl, 0·40 M-fructose or 0·16 M-glucose[161]	√		
2002	Se-deficient laying hens showed preference for a high-Se diet possibly due to learned aversion to a low-Se diet[162]	√		
2004	First draft of the red jungle fowl (*Gallus gallus*) genome released[67]; cockatiels were able to sense, monitor and avoid intake of potentially toxic compounds[163]; European starlings rejected garlic oil, decreasing intake even during feed deprivation[164]	√		√
2005	Chickens consumed a higher proportion of control than quinine- or denatonium benzoate-flavoured crumbs[165]; chickens' avoidance of quinine was found to be mediated by taste, resulting in decreased feed intake[166]	√		
2006	Three bitter TR (T2R1 and 2 and 7) and no T1R2 (sweet TR in mammals) reported in the chicken genome[68,81]			√
2008	Age-related (day 1 to day 140) differences in taste buds in the palate, tongue and base of the oral cavity in chickens[27]; natural or toxic chemicals such as quinine made colour biases aroused in chickens[167]; red-winged blackbirds preferred umami- (L-alanine) to potentially bitter-flavoured feed with tannic acid[168]	√	√	
2009	Aversion to feathers bittered with quinine decreased feather pecking behaviour[44]	√		
2010	Broilers have been shown to have a higher number of taste buds (312 compared with 192) and higher bitter sensitivity than layers[28]; bitter taste-based adjustment of feed choices and intake to minimise toxin and maximise nutrient intake in European starlings[34]; gustducin mediates intracellular taste excitatory pathways and is a reliable marker for gustatory cells in chickens[71]; T1R1 is expressed in chicken hypothalamus with higher expression in fat compared with lean breeds[104]	√	√	√
2011	Blackbirds related pre- and post-ingestive effects with visual and gustatory cues to avoid toxins and obtain nutrients[9]; coating the feathers with distasteful substances significantly reduced feather consumption and plucking in laying chickens[45]	√		
2014	The T1R1/T1R3 is tuned to alanine and serine in chickens and swifts but to simple carbohydrates in hummingbirds[7]; a specific appetite for Ca was associated with increased level of non-phytate P in broiler chickens[59]; chicken T2R receptors are broadly tuned and compensate the low numbers compared with mammals[74]; pre- and post-hatching exposure to bitterness alters T2R gene expression in the palate and duodenum and decreased feed intake[79]; *ex vivo* chicken taste buds responded to bitter and umami tastants[80]; feed restriction resulted in increased L cells and GLP-1 compared with control in chickens[97]	√	√	√
2015	Chicken GPR120 documented as fat TR[63]; behavioural sensitivity to bitter compounds was associated with the activity of T2R1 in chickens[65]; the low number of functional T2Rs in birds found related to the amount of toxic compounds in avian diets[76]; AA supplement (methionine, lysine) decreases the number of GLP-1-immunoreactive L-cells in the ileum compared with control[98]; umami, bitter and sweet TR and their downstream genes were found to be expressed in oral and GIT tissues in chicken embryos[105]; umami TR found to be expressed in the mouth and GIT and umami tastants increased feed intake in chickens[106]; GPR43 (fatty acid receptor) was found expressed in intestinal and other tissues and twenty-three genes encoding GPR43 paralogues were found in the chicken genome[107]; promiscuity profile of bitter ligands for T2R in chickens is similar to that of humans and frogs[169]		√	√
2016	Chickens found likely to sense sweetness through T1R2-independent mechanisms[8]; vimentin and α-gustducin were validated as markers of taste cells in chickens and allowed the unveiling of 507 taste buds in the palate and 260 in the base of the oral cavity (a total of 767) which increases the measures from previous publications[25,72]; CaSR was expressed in oral tissues and activated by Ca²⁺ in a dose-dependent manner in chickens[90]; GPR120 and CD36 were expressed in chicken oral cavity and GIT with fatty acids identified as potential agonists[93]; α-gustducin and α-transducin cells were located in chicken GIT epithelium[108]; quinine conditioning changes preference from big to small prey in chickens[170]	√	√	√
2017	Slow-growing broilers showed higher appetite for alanine, aspartic acid and asparagine (all non-essential) compared with fast-growing broilers in a double-choice test[53]; *in vitro* thresholds for bitter compounds were related to *in vivo* sensitivity but could not predict aversive behaviour in chickens[64]; two of the three chicken T2R (T2R1 and T2R7) were found to be active in oral tissues[66]; *in ovo* injection of 1 % arginine increased ghrelin and GLP-2 secretion, expression of jejunal T1R1/T1R3, CaSR and GPRC6A, and growth in 21-d-old broilers[99]	√	√	√

TR, taste receptor; AA, amino acid; MCT, medium-chain TAG; T2R, taste receptor family 2; T1R, taste receptor family 1; GLP, glucagon-like peptide; GPR, G-protein receptor; CD36, cluster of differentiation 36; GIT, gastrointestinal; CaSR, Ca sensing receptor.
* These reports are in German and have been reviewed by Berkhoudt (1992)[20].

published to date. The first traceable studies on the avian taste system refer back to more than 130 years ago and consisted of an anatomical examination of the avian oral cavity by Merkel (1880)[15] who failed to find taste buds. Botezat and Bath[16–19] were the first to report taste buds on palatal and mandibular areas of the oral cavity in several bird species. All these early reports were published in German and were reviewed in a book chapter by Berkhoudt (1992)[20].

Chicken taste buds were shown to have common morphological and anatomical features together with some cellular and developmental differences compared with other vertebrates[21–23]. Based on a few bird species studied to date (i.e. chicken, turkey, pigeon, etc.), it seems that taste buds are located mainly in the posterior tongue and pharynx as well as in the upper palate and base of the tongue, but not in the highly keratinised anterior and central tongue as is the case in mammals[6,24]. The most recent studies using molecular biology techniques showed that broiler chickens had 507 taste buds in the palate and 260 in the base of the oral cavity[25]. Ganchrow & Ganchrow (1985)[26] reported only a total of 316 taste buds in chickens, a number which has been used as a reference until recently as it appears to have underestimated the density of the avian taste sensory network. The palate of chickens has the highest number of taste buds compared with the other regions of the oral cavity, while broiler chickens have higher numbers than the egg-laying breeds[25,27,28]. Finally on anatomic structures, the chorda tympani nerve has been identified to be involved in chicken taste bud innervation[29,30].

The taste sense of the chicken plays a key role in the initial choice of feed and the level of feed consumption and growth[31–33]. Skelhorn & Rowe (2010)[34] showed that bitter taste-driven dietary selection in European starlings was essential in maximising nutrient while minimise toxin ingestion. Taste perception has been frequently targeted to try to improve feed intake, growth performance, mortality and feed conversion ratio in poultry[5,35–37] (Table 1). Additionally, taste-driven behaviours have also been studied to prevent economic losses in agricultural production due to birds damaging cereal and fruit production[38,39]. For example, fruits have been successfully protected against bird damage by increased sucrose content or by using coniferyl benzoate, a compound known to be bitter to avian species[40–42]. Furthermore, compounds known to be bitter to humans (quinine, garlic oil, almond oil, clove oil, magnesium chloride) have been successfully used to reduce feather pecking incidence in laying hens[43–45]. A decreased feed intake was also observed by adding jojoba oilseed to the diet, presumably caused by bitter taste aversion[46].

On the other hand, water deprivation of 2–6 h decreased the averseness to a quinine solution in chickens which was related to changes in taste sensitivity due to dry mouth[47,48]. It is tempting to speculate that under water scarcity (drought) the abundance of foods available may decrease and birds may need to be more tolerant to low-quality grains and fruits.

Other main taste-related events found in chicken literature include amino acid (AA) sensing. Initial work showing AA sensing in chickens studied AA preferences of limiting essential AA. A maize–soyabean meal diet supplemented with 4 % lysine was preferred over the same supplementation of methionine, threonine and arginine[49]. Similarly, broiler chicks were found to prefer a balanced diet containing synthetic AA compared with a similar diet deficient in lysine, methionine and tryptophan[50]. In addition, glutamic acid (L-Glu) received considerable attention as well, potentially related to umami taste. For example, L-Glu increased feed intake and growth in broiler chickens fed a low-crude protein diet[51]. However, excess dietary L-Glu may decrease appetite[52]. Recently, Niknafs et al. (2017)[53] reported that AA preference was related to the rate of growth in broiler chickens: slow-growing broilers consumed 64 % more of a non-essential AA (alanine/aspartic acid/asparagine)-supplemented diet compared with fast-growing broilers[53]. In addition, broiler chickens lowered their feed intake when the diet was supplemented with synthetic AA compared with a diet containing soya protein isolate[54]. The authors speculated that taste played a major role explaining this behaviour but post-ingestive effects were not properly considered.

Some studied avian species have shown preference for Ca-rich feed ingredients such as bones, shells and grit, which are rich in Ca[55]. Both broiler and laying chickens have a specific appetite for Ca, and they can meet their Ca requirement by consuming from a separate source in a choice feeding scenario[56–58]. Such specific appetite was also reported to be associated with the level of dietary non-phytate P[59]. Taste cues may play a key role in recognising Ca-deficient and -supplemented diets by chickens, and it has been reported that Ca-deficient chicks rejected calcium lactate solution due to aversive taste[60,61].

Finally, fat perception and consumption may have strong implications in poultry nutrition. Chickens were shown to increase feed intake of a high-added fat compared with a low-fat isoenergetic diet[6,62]. In addition, chickens showed a higher intake of a long-chain TAG compared with a medium-chain TAG-supplemented diet. Interestingly, such preference was inhibited after tongue paralysis, suggesting the role of oral gustation in dietary fat preferences[36]. Similarly, chickens were also reported to prefer oleic and linoleic acids from a maize oil-rich diet following a double-choice paradigm[63]. However, these results need to be interpreted with caution because of the long-term assay (7 h) together with the use of mineral oil (potentially toxic at high inclusion levels) in the reference diet.

In summary, the chronological review of the taste-related anatomy and feeding behaviour in chickens shows a long delay (50 years) in the discovery of the taste system (taste buds) in birds compared with mammals, probably related to the lack of taste papillae and to the initial focus on the bird tongue which is mostly deprived of taste-related anatomical structures[20]. However, in recent years research highlighting the association between taste-related feeding behaviour and cellular mechanisms in chicken has been abundant[64–66]. On the other hand, the advent of the sequencing of the red jungle fowl genome in 2004 introduced a new area, genetics and genomics, which has significantly changed the profile of research on avian chemosensory science ever since[67]. Thus, novel research tools have been applied to chicken chemosensory research including RT-PCR, functional heterologous expression assays, immunohistochemistry combined with scanning electron microscopy, and

three-dimensional image reconstruction, which has allowed improving our understanding of the molecular mechanisms of chicken taste.

Nutritional chemosensing in chickens: the molecular inside to taste

The availability of the chicken genome as a model opened up the research field of avian taste and nutrient sensing to the molecular underpinnings (Table 1). Lagerström *et al.*[68] identified 557 G protein–coupled receptor (GPCR) genes forming part of the chicken genome of which more than forty might be directly related to taste and nutrient sensing, as summarised in Table 2[6,68–70]. Some of the early works involved the downstream taste cellular signalling using vimentin and α-gustducin as molecular biomarkers for labelling and visualising chicken taste sensory cells[25,71–73]. Studies on the early development of taste buds showed profound differences between human subjects and chickens. Human taste bud cells originate from epithelial cells while in chickens they are of mesenchymal origin[73]. Interestingly, based on their unique migratory properties, mesenchymal cells play a fundamental role in embryonic development. Thus, it is tempting to speculate that taste sensory cells in chickens have the potential to spread, reaching a wider distribution in body tissues than in humans or mice (see the 'Extra-oral taste receptors mediating feed intake in poultry' section of the present review).

Generally speaking, bird species that have been studied so far have shown a lower number of bitter taste receptors (T2R) than some other vertebrates studied to date[6]. Chickens have only three bitter taste receptor genes: T2R1, T2R2 and T2R7[64,68,74]. Using heterologous cell expression systems and *in vivo* double-choice trials, specific agonist and antagonist ligands of the three chicken genes have been confirmed[64,66,74]. In particular, caffeine was shown to stimulate the T2R2 chicken receptor and elicit a negative preference in chickens at 10 mM or higher, but potential confounding stimulation of other receptors was not assessed[68]. In addition, the results reported by Dey *et al.*[66] showing no preferences for 3 mM-caffeine suggest that the affinity for the chicken T2R2 may be relatively low or that the gene may not be fully functional in

chickens. Moreover, there is a wide variation in the number of bitter taste receptors (T2R) between avian species, varying from one reported for domestic pigeons to eighteen for the white-throated sparrow[75,76]. Such diversity in the T2R repertoire in birds has been related to reflect species differences in nutritional needs and the adaptation to ecological niches[77,78]. Despite having only three bitter taste receptors in chickens, there is no evidence of an evolutionary contraction of the gene pool[77]. In addition, the relatively low number of taste receptors in chickens did not result in a decreased functionality and relevance of bitter taste since these receptors were shown to be widely tuned[74]. Hirose *et al.* (2015)[65] showed a direct association between behavioural responses to bitter tastants and the level of activity of the T2R1. Furthermore, before and/or after hatching exposure to bitterness altered the expression of bitter taste receptor genes in the palate of chickens, leading to decreased feed intake[79].

In vitro studies using cell reporter systems expressing chicken T1R1 and T1R3 receptors confirmed that these receptors respond to umami agonists to a similar extent seen in mice[7,80]. In contrast, chickens lack T1R2, one of the dimers of the sweet taste receptor gene in mammals[68,81]. The latter seems to explain the lack of response to sweet tastants in several studies conducted in chickens[82,83]. However, preference for carbohydrates including sugar in poultry has been reported in many studies[84–87]. In the mouse, a T1R2-independent pathway involving oligosaccharidases and the glucose transporter SGLT-1 in taste buds has been recently described[88]. A similar mechanism may be hypothesised in chickens[8]. Alternatively, it has been shown that some birds, such as the hummingbird, have adapted the umami receptor T1R1 to mainly perceive carbohydrates (and presumably sweetness)[7].

Table 2 summarises the array of mammalian nutrient sensors found to be expressed in the oral cavity of chickens (T1R1/3, Ca sensing receptor (CaSR), G-protein receptor (GPR) 120, T2R and cluster of differentiation 36 (CD36)). For example, the taste system seems to play a role in the regulation of Ca intake which is probably mediated by the CaSR and T1R3 in several mammals and chickens[89–92]. Finally, the long-chain fatty acid receptor GPR120 was found expressed in the palate of chickens which is speculated to be associated to oleic and linoleic acid sensing[63].

Table 2. Chicken nutrient-sensing genes (G protein-coupled receptors; GPR) identified based on homology with mammalian genes and mRNA expression data

Category	Nutrient	Mammalian genes	Chicken homologue genes
Energy	Sugars	*T1R2/T1R3, SGLT1*	*T1R3, SGLT1*
	SCFA	*GPR41, GPR43*	*GPR41, GPR43*
	Medium- and long-chain fatty acids	*GPR40, GPR120*	*GPR120*
Protein	Peptides	*GPR92/93*	*GPR92*
	L-Phenylalanine and L-tryptophan	*CaSR, GPR139*	*CaSR, GPR139*
	Other L-amino acids	*GPRC6A*	*GPRC6A*
	L-Glutamic acid	*T1R1, T1R3, mGluR*	*T1R1, T1R3, mGluR*
Minerals	Ca	*CaSR*	*CaSR*
	Na*	*eNaC*	*eNaC*
Organic acids	High [H+]*	*PKD1L3, PKD2L1, HCN*	*PKD2L1, HCN*
Water	Grain hydration*	*Aquaporins*	*Aquaporins*

T1R, taste receptor family 1; *SGLT1*, sodium–glucose cotransporter 1; *CaSR*, Ca sensing receptor; *mGluR*, metabotropic glutamate receptor; *eNaC*, epithelial sodium channel; *PKD1L3*, (protein coding), polycystin 1 like 3; *PKD2L1*, (protein coding), polycystin 2 like 1; *HCN*, hyperpolarisation-activated cyclic nucleotide-gated.
* These receptors have been defined as membrane channels and do not belong to the GPCR super-family.

In addition, the fatty acid transporter CD36 has also been reported to sense fatty acids in the oral cavity of chickens[93]. However, to date, taste perception of fatty acids in chickens has not been clearly demonstrated and requires further investigations.

Overall, the nutrient receptor gene repertoire in the chicken highly resembles those of the human and mouse with a few important exceptions such as the low number of T2R and the absence of the T1R2. However, the widely tuned nature of the T2R genes advocates for a fully functional sense in the chicken to a similar relevance than in some mammals. In contrast, the lack of the sweet receptor in the chicken may indicate that T1R2-independent pathways exist to monitor simple carbohydrates such as glucose. Chemosensory science in avian species is only an emerging discipline and is lagging behind the knowledge in mammals. Given their implication in feed intake and nutrient appetite, there is an increasing need for studying and understanding the regulatory network and co-expression analysis of nutrient sensors. Finally, since avian taste sensory cells are of mesenchymal origin which, in turn, is related to a higher capacity to migrate during development than epithelial cells (the origin of mammalian taste sensory cells) it would be interesting to study if the avian sensory cells are more abundant than mammalian sensory cells outside the oral cavity.

Extra-oral taste receptors mediating feed intake in poultry

The expression of taste receptors and nutrient sensors in extra-oral tissues, such as the gastrointestinal tract (GIT), has been found to play key roles in food intake and appetite control. They have been involved in responses to the luminal content involving the secretion of hunger–satiety hormones such as glucagon-like peptide (GLP)-1, ghrelin and cholecystokinin (CCK)[13,94–96]. Chickens under feed restriction had higher numbers of GLP-1-containing intestinal L cells compared with unrestricted birds[97]. Similarly, a lower number of GLP-1-immunoreactive cells were found in chickens fed a methionine/lysine-supplemented diet compared with the control non-supplemented group[98], whereas *in ovo* injection of arginine increased the secretion of jejunal ghrelin and GLP-2[99]. In addition, dietary supplementation with medium-chain TAG increased CCK secretion and decreased feed intake in chickens[100]. Taste receptors and nutrient sensors expressed in the GIT have been related to sensing nutrients in luminal contents, resulting in the secretion of gut peptides mediating food appetite in some mammalian species. The main outcomes have been recently reviewed[94–96,101–103].

In an early work in chickens, Byerly *et al.* (2010)[104] demonstrated the presence of the umami taste receptor (T1R1) in the hypothalamus. The chicken T1R1 was expressed at higher levels in fat compared with lean broiler lines. Cheled-Shoval *et al.* (2014[79] and 2015[105]) reported the expression of both chicken T1R and T2R subfamilies in the GIT. The presence of umami taste receptors in the chicken's GIT was also cofirmed by Yoshida *et al.* (2015)[106]. In addition, the expression of fatty acid receptors GPR43, GPR120 and CD36 were also reported in the chicken's intestine[93,107]. Finally, α-gustducin and α-transducin cells have also been reported in the chicken's GIT[108].

Unpublished results from our group (S Niknafs and E Roura, unpublished results) targeted extra-oral AA sensors (T1R1/T1R3, CaSR, GPR92 and GPR139) and showed that they are significantly expressed in the chicken's GIT, being a higher expression of CaSR and GPR139 associated with higher feed intake and growth rate in broiler chickens. In addition, intestinal nutrient transporters have also been reported to sense nutrients[109]. In poultry, transporters for peptides, AA, glucose and fructose have been extensively studied[110–119]. However, their role as chemosensory mediators has yet to be fully described.

The role of nutrient sensors in the GIT has been unveiled in the mouse, rat and humans but current knowledge in avian species is scarce. The scenario depicted in the Introduction where the anatomy (and perhaps the function) of the chicken taste system is fundamentally different from in some studied mammals may be repeated regarding the role of taste receptors in the GIT. The existence of a network of sensory cells related to the enteroendocrine system underlines the relevance of nutrient sensors in the secretion of gut peptides. However, the hormonal control of appetite related to the gut–brain axis based on gut peptides has been shown to feature major differences between the chicken and mouse. For example, although ghrelin in humans and the mouse is an orexigenic hormone[120], it has been well documented to be anorexigenic in the chicken[121–127]. In contrast, peptide YY (PYY) and GLP-1 have an anorexigenic role in humans and the mouse, whereas in the chicken they seem to stimulate appetite[69,97,98,128,129]. Overall, what has been learned so far on chicken nutritional chemo-sensing shows an area with potentially profound implications in avian nutrition that needs further investigation, particularly regarding gut mechanisms and their functionality related to gut peptides and the hunger–satiety cycle.

Conclusion

The present review of the avian taste-related literature dismounts the long-sustained dogma that birds have a minor level of taste sensing. Chickens, and the other avian species studied so far, seem to taste different (not less) from mammalian species. The anatomical features reveal an evolution of the taste system in harmony with an oral cavity and deglutition mechanics requiring a slim long keratinised tongue incompatible with a sensing system on it (such as in mammals) which, in turn, found its place in the upper palate. The essential role of taste as the nutrient-sensing machinery in chickens seems to be close to the mammalian system except for carbohydrates (sweet in mammals) since the T1R2 gene was lost in evolution. Similarly, compared with mammals and most amphibians, chickens and the other avian species studied to date appear to have a smaller bitter taste receptor (T2R) repertoire. However, the low number of T2R genes may be compensated by their nature, tuned to sense a wide array of chemicals. Thus, AA and fatty acid sensing (and possibly Ca) seems to take the lead in nutrient appetites in chickens. However, the relevance of carbohydrates (i.e. glucose) should not be discarded in birds since chickens show an active T1R2-independent pathway and the umami gene T1R1 in some mammals responds to sugars in hummingbirds. The change in molecular roles from mammals to

some bird species like the hummingbird does not seem to be an isolated occurrence. On the contrary, gut peptides with appetite-enhancing properties in well-studied mammals like mice may suppress the appetite of birds and the other way around such as in the case of ghrelin, PYY and GLP-1. However, there is a lack of data regarding the regulatory genes and pathways orchestrating the control of feed intake in chickens. Studying the molecular and regulatory networks involved in nutrient-sensing mechanisms across the GIT and the central nervous system can partially explain the variation in feed intake within strains with the same genetics. In addition, little is known about genetic polymorphisms in taste receptors, nutrient sensors and their downstream effects that may affect feed intake regulation mechanisms in chickens, warranting further investigation.

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