

OPINION

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Comparative biology of taste: Insights into mechanism and function

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Abstract

Each animal lives in its own sensory world that is coordinated with its diet. In this brief review, we describe several examples of this coordination from studies of the sense of taste, particularly from species of the order Carnivora. This order includes species that are obligate carnivores (e.g., *Felis* species), omnivores, and strict plant eaters. Many of the obligate carnivores have lost function for sweet taste, presumably through relaxation of selection for eating sugars from plants. In contrast, the giant panda, which feeds almost exclusively on bamboo, retains sweet taste function but may have lost amino acid (umami) taste perception. Finally, mammals that have “returned” to the sea, such as sea lions, have experienced even more extensive taste loss, presumably as a consequence of adaptations to a diet of fish and other sea creatures swallowed whole. Future comparative studies will surely reveal important relationships between diet and molecular, cellular, and behavioral taste adaptations that will shed light on how evolution moulds sensory structure and function.

Keywords: Taste, Taste receptors, Comparative studies, Carnivora, Cats, Giant panda, Sea lion, Evolution

Each animal species lives in a separate sensory world that is coordinated with its behavioral ecology. A dramatic example of this occurs for the sense of taste [1] where sensory perception and diet choice are intimately intertwined.

The evolutionary basis for the existence of a small number of primary taste qualities (sweet, bitter, sour, salty, umami, and perhaps a few others) is that these qualities evolved to detect and motivate consumption of critical nutrients and detect and avoid potential poisons. It is widely believed that sweet taste evolved in animals that eat plants to detect energy-rich simple sugars such as glucose, fructose, and sucrose. In contrast, bitter taste presumably functions to insure that an animal avoids poisons; most poisons are bitter and most bitter substances are harmful although this relationship is not perfect. Salty taste is thought to enable detection of sodium, an absolutely essential mineral. When some species of animals become deficient in sodium—usually this occurs in herbivorous animals—a powerful appetite for salty taste is aroused. And for many species, salt is consumed even when there is no apparent need. For sour taste,

many have suggested that it is involved in the detection of the ripeness of fruits. Finally, the fifth basic taste, umami or savory, probably serves to signal amino acids and protein. This however remains speculative. Other classes of compounds may also interact with the taste system (e.g., fatty acids, calcium, starch), but they do not give rise to the (to humans) strong qualitative percept that the other five do.

To obtain a clearer understanding of the functional significance for these basic taste qualities, we have studied the order Carnivora. Our goal is to understand how taste receptors and taste perception in different species are related to different feeding ecologies with a particular focus on sweet compounds. For example, some Carnivora species are obligate carnivores (e.g., cats), whereas others are almost completely herbivorous, sometimes feeding on virtually a single plant (e.g., giant panda). If the function of sweet taste is to detect simple sugars in plants, we predict that animals that do not consume plants would not need/have sweet taste perception. By examining sweet taste perception across a number of species in this order, we can put this prediction to the test.

Many years ago, we [2] demonstrated that domestic and wild cats (*Felis* and *Panthera* species) are indifferent to all sweeteners tested but are highly responsive to

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certain amino acids and fats. We speculated that these species may not have the ability to perceive sweet (to humans) sugars. Following the discovery of the major sweet taste receptor, the T1R2 + T1R3 heterodimer (review: [3]), we demonstrated that the cat's indifference to sweeteners can be explained by the pseudogenization of the *Tas1r2* gene which encodes the T1R2 receptor. That is, the sweet taste receptor of the domestic cat as well as closely related wild cats such as lions and tigers has accumulated numerous germ-line mutations of the *Tas1r2* gene, thereby rendering the sweet receptor non-functional [4].

We next reasoned that other exclusively meat-eating species might also have an inactive form of this gene. Sequencing of the entire coding region of the *Tas1r2* gene from 12 Carnivora species revealed that seven of these species, all exclusive meat eaters, had independently fixed a defective *Tas1r2* allele [5]. Since these disabling mutations occurred at different places within the *Tas1r2* gene in each species, this loss of sweet taste function in multiple species in the Carnivora has occurred independently and thus repeatedly during their evolution. Behavioral tests of two of the genotyped species, the Asian otter (defective *Tas1r2*) and the spectacled bear (intact *Tas1r2*), were consistent with the genetic findings: The former showed no preference for sweet-tasting compounds, while the latter preferred sugars and some non-caloric sweeteners. These results indicate that the independent loss of a functional *Tas1r2* is widespread among obligate carnivores. We suggest that this loss is a consequence of the relaxation of selective pressures maintaining receptor integrity.

A striking study with birds provides additional support for the hypothesis that sweet taste exists to detect simple sugars. All birds apparently lack a homolog for the *Tas1r2* gene; this loss likely occurred as the non-avian reptile and bird lines split. Thus, it would seem that birds should not be able to taste sweet sugars. But if this were the case, how can one explain the behavior of avian species that consume sweet sugars such as hummingbirds? Baldwin et al. [6,7] provide one answer: The receptor dimer T1R1 + T1R3, the amino acid or umami receptor in mammals, has been repurposed in these bird species to detect simple sugars thereby opening a novel source of energy not available to many other birds. In sum, these studies provide strong support for the hypothesis that sweet taste perception exists to provide an ability to identify energy-rich sugars.

More recently [8], we conducted behavioral and molecular studies with giant pandas, animals that consume plants, but ones (bamboo) without abundant simple sugars. Would this member of the order Carnivora retain sweet taste perception, or would the absence of a need to find specific plants that taste sweet also result in

relaxed selection for maintenance of receptor function? We found that sweet taste perception is fully functional in giant pandas. Although giant pandas thus retain an avidity for sweet compounds, genetic evidence suggests that this species has lost umami taste perception [9], but as yet we know of no behavioral studies verifying this nor do we understand why this may have occurred and how widespread such loss might be.

Although loss of sweet taste seems common for animals that do not consume plants, are there species that have lost even more of the basic tastes? And if so, how can this be interpreted? Based on genetic studies, we [5] and others [10] have reported that many mammalian species that have returned to the sea (e.g., sea lions, dolphins, whales) may have independently lost function for several, perhaps all, taste quality perception. These genetic studies are consistent with anatomy (many of the species do not have identifiable taste cell structures) and behavior (many eat their food whole, without apparently "tasting" it). The factors responsible for this extensive loss of taste function in marine mammals remain to be determined.

In summary, these data dramatically illustrate how plastic the taste system is and, as illustrated through the sweet taste modality, how it has adapted to changes in diet as species evolved. Similar changes are likely in the other taste qualities. For example, it is likely that species differences in the repertoires of bitter receptors reflect different classes of poisons that these species are likely to confront [11]. Species variation in salt taste perception is also likely to be coordinated with diet. For example, it is possible that strict carnivores may not perceive NaCl in the same way as do herbivorous mammals since carnivores' all-meat diet likely provides sufficient Na⁺. Finally, as a third example, the human umami or amino acid receptor responds to only a few compounds (glutamate and a few others). However, this receptor acts as a more general amino acid receptor for rodents and other species. These species differences may also be explained by different feeding ecologies although this remains to be determined. Future comparative research will surely reveal many more interesting and important relationships between taste function, food choice, and diet.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

This review was written by both authors. Both authors read and approved the final manuscript.

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