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Mammalian Salt Perception and Preference

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ABSTRACT

Salt (NaCl) is ubiquitous in diets in many countries. Research at the Monell Center is involved in understanding the basic mechanisms underlying salt perception and preference from biophysical, physiological and behavioral perspectives. Animal model studies demonstrate that salt taste transduction involves a sodium channel in the taste bud. Control of salt appetite in animal models is determined by both genetics (inbred strains of mice differ in their avidity for salt) and by the physiological state of the organism (both sodium and calcium are involved in regulating salt appetite). For humans who often consume one or two orders of magnitude more NaCl than the presumed physiological requirement, considerable data support the view that the optimal level of salt in the diet is determined in part by the level an individual is currently consuming; increasing or decreasing customary salt intake, as long as the salt is tasted, increases or decreases, respectively, the preferred level of salt in food. While these data are consistent with a hypothesis that optimal salt preferences are learned, other data, from both animal models and human developmental studies, suggest that salt preference has an innate component. Furthermore, early experience with low or high salt diets may have a long-term impact on preferred salt levels. A preference for salt, like a preference for sweets, has an innate basis that can be modified by individual experience.

MAMMALIAN SALT PERCEPTION AND PREFERENCE

Salt (sodium chloride) holds a special place in human history. It has, when available, been used extensively in human cuisine, formed a fundamental unit of exchange, and even been a cause of war. Salt has commonly been taxed because of its universal usage and value. Utensils that contained salt were often elaborate and expensive.

Sodium is required for a variety of biological functions, including nerve conduction, blood pressure maintenance, acid-base balance, and muscle contraction. Its balance in the body is finely regulated. Excess sodium is usually excreted efficiently in the urine. Elaborate hormonal mechanisms exist in many organisms for conserving sodium when intake is restricted. Sodium deprivation is quickly followed in many vertebrate species by increases both in the activity of the renin–angiotensin system and in aldosterone production; these hormones are involved in mediating inhibition of urinary sodium excretion and thereby help conserve body sodium.

There is a major behavioral component in the maintenance of sodium balance. Herbivorous animals, whose diet of plants is relatively low in sodium, are known to travel long distances to gain access to salt-rich earths or other sources of sodium. In contrast to herbivores, carnivores would presumably never suffer sodium deficiency, because their diet of muscle, viscera and blood contains relatively high amounts of sodium. The extent to which omnivorous animals would be exposed to the stress of sodium deficiency is unclear. The primate ancestors of humans were likely to have been almost completely vegetarian and were thereby exposed to a potential sodium deficiency (Denton, 1984). Consequently, it is not surprising that neural, hormonal and behavioral regulatory systems have evolved in many herbivorous and omnivorous species to ensure the discovery, recognition and consumption of sufficient sodium to meet or exceed biological requirements. Those mechanisms may also be responsible, in part, for consuming much more salt than is required.

SALT TASTE: RECEPTION AND TRANSDUCTION

A focal point in these systems for regulating sodium balance is the sense of taste. Taste receptor cells are located on the tongue and oropharynx.

These cells are innervated by branches of the 7th, 9th and 10th cranial nerves.

Most investigators believe that saltiness is one of a small number of primary taste qualities, which also include sweet, sour, salty and perhaps umami. Neurophysiological studies confirm the specificity and distinctiveness of salt perception (e.g., Boudreau et al., 1983; Frank et al., 1983).

Recently there have been significant advances in our understanding of the mechanisms by which the taste of salt is transduced. Apparently, at least one component of the stimulus-receptor interaction involves movement of the sodium ion into the taste cell, through an amiloride-blockable ion channel, which in turn promotes depolarization of the cell, thereby firing the taste nerve (DeSimone et al., 1981). According to this model, the sodium ion flows passively through a specific sodium channel thereby increasing the positive charge within the cell. This results in firing of the taste nerve. Recently, it has been suggested that the reason only sodium chloride and lithium chloride have a pure salt taste is because the chloride anion has the property of being able to move through the tight junctions between the taste cells along with the sodium, reaching channels inaccessible to ions that cannot penetrate the tight junctions. For other anions such as acetate a negative charge builds up outside the taste cell and a positive charge within the taste cell apparatus presumably resulting in off tastes of such substances as sodium acetate.

These biophysical studies suggest that, unlike the case for sweet, a practical salt substitute is unlikely since the mechanism is so specific to sodium and lithium. However, it is known from a variety of studies on these sodium channels that there are substances that block them thereby presumably reducing saltiness (Schiffman et al., 1983; Heck et al., 1984; Brand et al., 1985). Conversely, it is possible that there are substances which will open these channels wider, acting as salt enhancers. No such substance with practical significance has yet been identified, however, but this constitutes a very active area for research.

REGULATING SALT INTAKE: ANIMAL STUDIES

Many animal model studies have demonstrated that when animals are depleted of sodium they will seek out salt to replenish their need. The ability to associate a need for sodium with the taste of salt is innate. Although there are clinical examples of this phenomenon in humans, it is very rare for an individual to become truly sodium deficient. Experimental studies with adults have shown only modest increases in the desire for salt following depletion with low sodium diets, heat or drugs (see Beauchamp et al., 1991 for extensive discussion).

Recently, Tordoff et al. (1990) has shown that when rats are moderately depleted of calcium, they increase their salt intake markedly. Neither the mechanism by which this occurs nor the applicability to humans is known; this is currently under investigation. Tordoff has suggested that high salt intake among children, some racial groups and others under calcium stress could be accounted for by these mechanisms.

In addition to dietary factors, genetic differences may account for some of the large individual differences seen in salt preference and intake. Recent studies have been conducted using two highly inbred strains of mice. Within a strain, all individuals of the same sex are genetically identical. Mice of one strain (called C57) tend to reject salt solutions relative to water at all concentrations above threshold whereas mice of another strain (called 129) tend to prefer salt solutions to water at moderate concentrations, close to those that humans often find most palatable in such foods as soups (e.g., Bertino et al., 1983). When individuals of the two strains are mated, forming the first filial generation, the F_1 generation, offspring tend to be intermediate (Fig. 1). Mating these offspring to produce the second filial generation (F_2) yields approximately 1/4 of the mice who tend to reject salt solutions, whereas 3/4 are indifferent or prefer these (Fig. 2). This pattern of inheritance of salt preference could suggest that a major gene effect

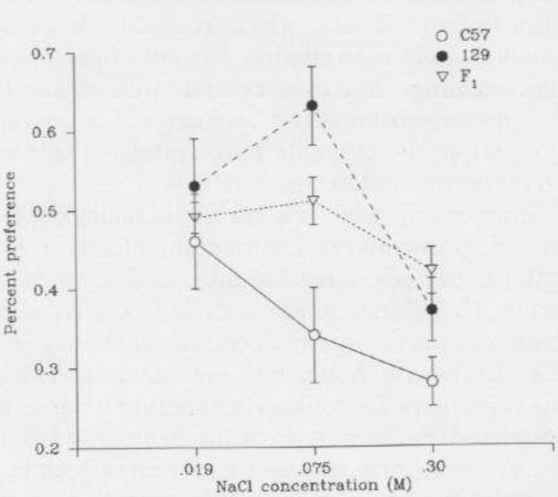

Fig. 1. Percent preference (amount of salt solution consumed divided by amount of salt solution plus water consumed) in 48-h 2-bottle preference tests for 2 inbred strains of male mice (129 and C57BL/6) and their F_1 hybrid generation. Mice of the C57 strain tend to reject salt relative to water at moderate to strong concentrations whereas 129 mice prefer salt to water at 0.075 M. The F_1 generation is between the two.

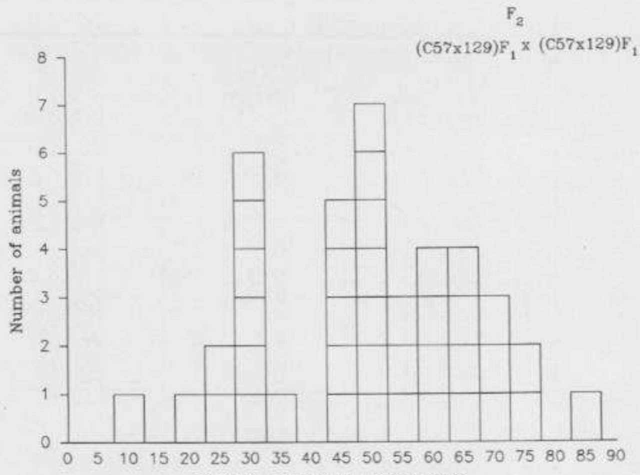

Fig. 2. Percent preference for 0.075 M NaCl for 40 male F2 generation mice [C57×129)F_1 × (C57×129)F_1]. Each box represents data from 2 tests for a single mouse. The distribution appears to be bimodal with approximately 1/4 rejecting NaCl relative to water thereby resembling the C57 parental strain.

plays a role (Beauchamp, 1989). Work is currently underway to investigate this issue and to identify the gene(s) involved as well as to understand their mode of action.

REGULATION OF SALT INTAKE: HUMAN STUDIES

Humans tend to consume one to two orders of magnitude more salt than is physiologically required. What maintains this high salt intake is not known. We have taken two approaches to investigate this: experimental studies with adults and developmental studies on infants and children.

Experimental studies with adults

Experimental studies have examined the effects of alterations in consumption of salt on salt taste preference. The amount of salt in food required to make the food taste best (that is, the optimal level) has been measured. For many foods, very low levels of salt and very high levels are not as desirable as moderate levels and, for individuals, there exists an optimal salt level. A series of studies (review: Beauchamp et al., 1991) has demonstrated that if salt intake is reduced by about 45% over a period of time, the optimal level of salt in foods declines. The amount of salt required to optimize food flavor is decreased to about 50–60% of the prediet amount (Fig. 3). Thus, if the optimal level of salt in soup for an individual was 1.2% (approximately 0.2 M) while he or she was on a diet containing 140 meq Na/day, which translates into approximately 8 g of salt per day, decreasing sodium consumption to about 80 meq/day would result, on average, in a reduction in optimal salt levels in soup to 0.6–0.7%. Importantly, this change is gradual, taking probably 2–3 months to reach asymptote.

It is likely that this change in preference is due to the decreased experience of tasting salty foods rather than to a physiological response to the change in amount of sodium the body must handle for three reasons. First, the gradual nature of the effect would

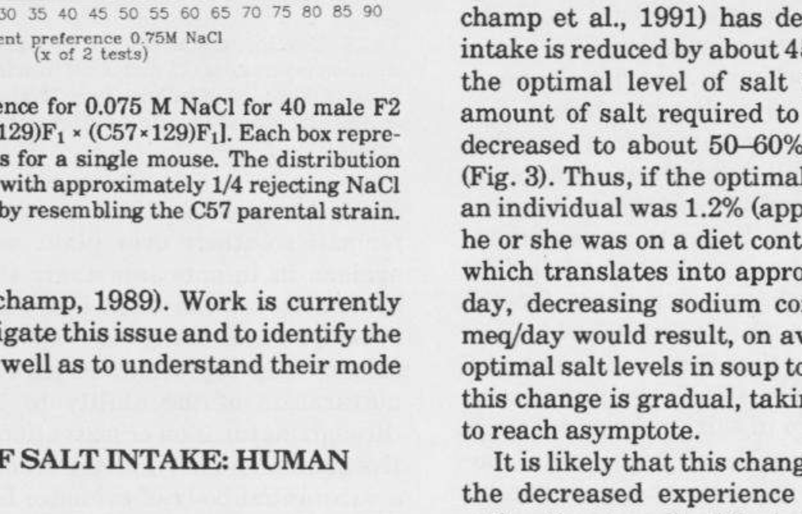

Fig. 3. Amount of sodium consumed by adult human subjects initially (I) and during the experimental manipulation (E) in 3 studies. Whether there was a change in the optimal level of salt as a consequence of manipulation of consumption is indicated below each pair of bars. The stipplied area of the boxes in Study 3 represents the amount of added salt from shakers. See text for more detail and appropriate references.

suggest experience plays the major role, because physiological responses to changes in sodium consumption, for example, changes in the hormones of sodium balance, are much more rapid. Second, we found that if salt consumption was increased by requiring subjects to add approximately 10 g of salt to their food, optimal levels of salt in food also increased. However, this change in optimal level was more rapid than when salt intake was reduced. If the same amount of additional salt was consumed as tablets and thus not tasted, there were no changes in taste preferences. Apparently, a sensory adaptation to different levels of salt accompanies a change in salt intake. To some extent, people like the level of salt they taste rather than, or in addition to, choosing the intensity of the taste of salt they like.

The third reason for believing that this change in optimal salt level following dietary change is a psychological phenomenon comes from another study in which dietary salt was reduced by approximately 50%, but continued use of table salt from a salt shaker was permitted. Under these conditions, individuals' use of added salt more than tripled but did not increase enough to compensate for the amount removed. In fact, they only replaced about 30% of the decrement so that there was an overall decrease of approximately 40% in sodium intake. Yet, there was no change in salt preference. In this instance, salt was presumably added "to taste", implying that although the salt content of their regular food was in a range that the subjects found palatable, it was unnecessarily high, probably because it was dispersed throughout the food, rather than all being on its surface and easily accessible to the taste receptors.

In sum, a substantial number of studies support the conclusion that changes in optimal salt taste preferences following changing of salt intake are mediated by hedonic-cognitive expectations based on current dietary experience. Physiological changes associated with alterations in the amount of NaCl available to the body do not appear to play a major role.

Developmental studies

Data concerning the early development of salt preference and how experiences may serve to modify or perhaps permanently established heightened preferences are conflicting and confusing. Newborn infants are either indifferent to or avoid moderate to high concentrations of saline solution relative to water Crook, 1978; Desor et al., 1985). By the time children are 2–3 or more years of age, preferences for salty foods over those same foods without salt are common. These two observations have led some to conclude that salt preference is learned, although that conclusion does not necessarily follow. We (Beauchamp et al., 1985) showed that a preference for salt solutions over plain water, although not evident in infants less than 4 months of age, is evident in infants 4–23 months of age (Fig. 4). A developmental change in response to salt in human infants may represent, in part at least, postnatal maturation of the ability to taste salt perhaps through maturation or activation of amiloride sensitive channels. This interpretation is consistent with a substantial body of evidence from animal models that demonstrates that the neurophysiological response to salt exhibits a postnatal developmental change. In both rats and sheep, responses to salt in newborn animals are less robust than responses in adults (review: Hill and Mistretta, 1990).

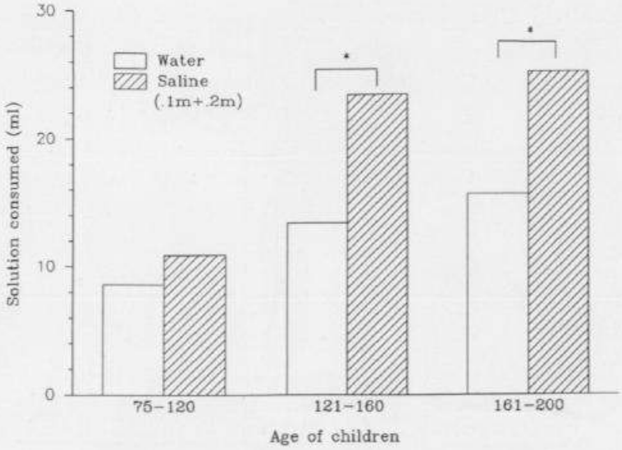

Fig. 4. Developmental change in ingestion of water and salt solution (average of 0.1 and 0.2 M) during very brief preference tests of 3 groups of infants (n = 18/group) at 3 ages. *$p<0.01$ comparing water to salt solution intake. See text for more detail.

Even if there is a postnatal maturation of salt taste perception and preference, experience with salt could modulate this preference in infants just as it does with adults. There are reports of a correlation between exposure to salted food and relative preference for saltiness in that food; however, these data are not conclusive as they are based on data from very few infants (e.g., Harris and Booth, 1987). Further longitudinal studies on the development and early modification of salt taste preferences are needed. In particular, the issue of the relationship between level of exposure to salt and salt preference should be explored at several ages to understand the origin of the high salt preferences relative to need seen in so many humans around the world. In this regard, we and others have shown that young children and adolescents actually prefer higher levels of salt in food than do adults. It is unclear why this is the case, although it is possibly due to altered nutritional requirements during growth.

CONCLUSIONS

1. The initial events in salt taste are becoming clear; although a salt substitute is unlikely, a practical salt enhancer may be developed in the future.

2. There are multiple regulators of salt intake, some of which are innate and some of which are mainly determined by environmental factors.

3. Innate factors include an inherent liking for the taste in many species including humans. Individual differences within a species may be under genetic control.

4. Nutritional factors, for example sodium and calcium status, partially control salt consumption in animal models and perhaps in humans.

5. For adult humans, optimal levels of salt in food are, in part, a function of current dietary intake. Optimal levels can be altered by changes in the saltiness of the diet an individual consumes.

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