Ontogeny of taste preferences: basic biology and implications for health1–5

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ABSTRACT

Health initiatives address childhood obesity in part by encouraging good nutrition early in life. This review highlights the science that shows that children naturally prefer higher levels of sweet and salty tastes and reject lower levels of bitter tastes than do adults. Thus, their basic biology does not predispose them to favor the recommended low-sugar, low-sodium, vegetable-rich diets and makes them especially vulnerable to our current food environment of foods high in salt and refined sugars. The good news is that sensory experiences, beginning early in life, can shape preferences. Mothers who consume diets rich in healthy foods can get children off to a good start because flavors are transmitted from the maternal diet to amniotic fluid and mother’s milk, and breastfed infants are more accepting of these flavors in contrast, infants fed formula learn to prefer its unique flavor profile and may have more difficulty initially accepting flavors not found in formula, such as those of fruit and vegetables. Regardless of early feeding mode, infants can learn through repeated exposure and dietary variety if caregivers focus on the child’s willingness to consume a food and not just the facial expressions made during feeding. In addition, providing complementary foods low in salt and sugars may help protect the developing child from excess intake later in life. Early-life experiences with healthy tastes and flavors may go a long way toward promoting healthy eating, which could have a significant impact in addressing the many chronic illnesses associated with poor food choice. Am J Clin Nutr doi: 10.3945/ajcn.113.067694.

INTRODUCTION

Many health initiatives, including “Let’s Move!” launched by the White House in 2010, are attempting to end the epidemic of childhood obesity within a generation through new steps to encourage good nutrition and exercise (1). Recommendations include that both adults and children limit consumption of salt, fat, and simple sugars, which have sensory properties that we find particularly palatable, and eat more fruit and vegetables, the latter of which sometimes taste bitter (2–4).

A major challenge for these health initiatives is that neither adults nor children are complying with these recommendations (5, 6). The 2002 and 2008 Feeding Infants and Toddlers Study, designed to update our knowledge on the feeding patterns of American children, found that 1 in 4 toddlers did not consume even one vegetable on a given day (5–7) and instead, like older children (8–11), were likely consuming French fries, sweet- and salty-tasting snacks, and sweet beverages (5, 6). By the second year of life, not 1 of the top 5 vegetables eaten was a dark-green vegetable (5, 6). Thus, it is not surprising that the recently launched Healthy People 2020 lists as one of its goals (Goal NSW-15) an increase in the variety and contribution of vegetables to the diets of the population, including its youngest members (4).

How can we account for patterns of food choice that seem antithetical to health and for the difficulties in changing them? Two factors conspire to predispose some children to consume obesogenic diets: 1) inborn, evolutionarily driven taste preferences and 2) detrimental consequences of not being exposed to flavors of healthful foods early in life (see references 12–14 for previous reviews). Children have sensory systems that detect and prefer the once-rare calorie- and mineral-rich foods that taste sweet or salty (15), while rejecting the potentially toxic ones that taste bitter (16, 17).

This review highlights research that shows some of the biological drives of food acceptance during infancy and childhood and how early-life experiences interact with inherent plasticity of the chemical senses to mold preferences for foods. We focus on scientific evidence suggesting that early experience can influence what foods are preferred, as well as the ontogeny of sweet, salty, and bitter, the tastes that 1) have been most extensively studied, 2) are directly involved in choices of specific foods of concern (sweet and salty foods and bitter-tasting vegetables), and 3) exhibit age-related changes in function.

IMPORTANCE OF EARLY-LIFE EXPERIENCES

Early-life exposures—both biological and social—explain trajectories of health in adulthood decades later (18). In particular, excessive intakes of foods high in salt (sodium chloride)
and refined sugars early in life cause or exacerbate a number of illnesses and conditions in adulthood (19–22), such as obesity, metabolic syndrome, and mortality from cardiovascular disease. Such long-lasting impacts of early nutrition on health underlie the life-course approach taken in many medical fields, as well as the suggestion that both preventive interventions and further scientific inquiry should focus on early life (21, 23, 24).

Early experience has far-reaching effects on behavior. Emerging research has shown the existence of postnatal periods when the developing brain has heightened sensitivity to environmental influences (25)—epochs of brain plasticity when the early environment can shape neural circuits and thus behaviors. Beginning very early in life, sensory experiences shape and modify flavor and food preferences (26–29).

Although humans generally have inborn, positive responses to sugar, and perhaps salt, and negative responses to bitter, genetically determined individual differences also exist and interact with experience to ensure that children are not genetically restricted to a narrow range of foodstuffs (see references 12 and 30 for review). Thus, early experiences with nutritious foods and flavor variety may maximize the likelihood that, as children grow, they will choose a healthier diet because they like the tastes and variety of the foods it contains.

In support of this hypothesis, longitudinal studies have shown that food habits established during infancy track into childhood and adolescence (31–35) for both nutrient-dense and nutrient-poor foods (34). Such dietary patterns, which begin to be identified during childhood (36), are significant determinants of the quality of the adult diet (37, 38). The most apparent period of change in dietary patterns was evident during early childhood (35), with new foods more likely to be accepted when children are 2–3 y of age compared with older ages (31). After the age of 3–4 y, reported dietary patterns/food habits remained quite stable, further highlighting the importance of getting children on the right track from the initial stages of learning to eat (≤3 y) (see also reference 33).

Most studies that tracked dietary patterns/food habits have been correlational in nature and thus, some have argued, inconclusive (39). Nevertheless, the evidence suggests positive consequences of healthy dietary trajectories from infancy to adulthood and how learning to like “healthy” foods is modifiable and begins early in life. During childhood, the strongest predictors of what foods young children eat are 1) whether they like how the foods taste, 2) how long they were breastfed and whether their mothers ate these foods, and 3) whether they had been eating these foods from an early age (31, 35, 40–42). An important area for future research includes randomized controlled trials on early diet that focus on both caregivers and children (eg, references 43 and 44).

BIOLOGY OF THE CHEMICAL SENSES

Flavor, a powerful determinant of human consummatory behavior throughout the life span, is a product of several sensory systems, most notably those of taste and smell (odors perceived retronasally). The anatomically independent flavor senses are well developed at birth and continue to change throughout childhood and adolescence, serving as gatekeepers throughout the life span (45), controlling one of the most important decisions an animal makes: whether to accept or reject a foreign substance. They also inform the gastrointestinal system about the quality and quantity of the impending rush of nutrients or toxins (46).

The tastes of foods that children initially either prefer (eg, sweet, salty foods) or reject (eg, bitter-tasting foods, including some vegetables) in part reflect their basic biology. Age-related changes in taste perception and preference, documented by experimental research during the past century, indicate that the rewarding properties of sweet and salt are more pronounced during childhood. Many drugs of abuse coopt ancient brain reward systems that underlie hedonics of salt taste (“our primordial narcotic”) (47) and sweet taste (“our oldest reward”) (48).

Sweet

The preference for sweet tastes, which is present early in life, is remarkably well conserved in primates (49). At birth (and perhaps even before), the ability to detect sweet tastes is functioning and interacting with systems that control affect (49–51). Infants born preterm and tested between 33 and 40 wk postconception produced stronger and more frequent sucking responses when offered a sucrose-sweetened latex nipple compared with an unsweetened latex nipple (50). Within hours after birth, newborns differentiate varying degrees of sweetness and consume more of a sugar solution than water (52). When a sweet solution is placed in the oral cavity, infants relax the face and sometimes smile (49, 51).

Psychophysical studies have shown that the preference for sweet taste is universal and evident among children around the world (53, 54). Both cross-sectional and longitudinal studies have shown that preferences for sweets remain heightened throughout childhood (55–58) and early adolescence (53, 55), declining to adult levels during midadolescence (53, 55). In one of the largest studies on sweet preference (930 participants), which analyzed data for the NIH Toolbox Initiative, children selected a 0.54-mol sucrose/L concentration as their most preferred (55), a concentration equivalent to 11 teaspoons (~44 g) of sugar in an 8-ounce glass of water—nearly twice the sugar concentration of a typical cola (0.34 mol/L).

Sweet taste in the mouth can also blunt expressions of pain in children (59) and acts as an opioid receptor–dependent pain-reducing agent. Its ability to act as an analgesic has been investigated extensively in preterm and term infants (see reference 60 for review) and to a lesser extent in children (57, 61, 62). Sweet taste is effective in reducing spontaneous crying and pain in preterm and term infants during an array of painful procedures, such as a heel lance, venipuncture, or intramuscular injections (60). Children can keep their hand in a cold-water bath longer while tasting sweet (57, 61, 62), and the more they like sweets, the better its analgesic properties (57).

Salt

Children also prefer substantially higher concentrations of salt than do adults, and adding salt to foods can drive consumption (56, 63, 64). However, newborns generally do not react strongly to moderate concentrations of salt (51, 63); salty taste detection appears to develop later, perhaps at ~2–6 mo (63). Compared with sweet preferences among children (12), salt avidity is more complex and less understood.

Salt preference is affected by prenatal experiences (65–67) and apparently more plastic than is sweet preference. Infants born to women with moderate to severe morning sickness showed
significantly higher intake of salt solutions at 4 mo of age than did those whose mothers reported having no more than mild morning sickness (66). Adolescents and young adults preferred higher concentrations of salt in a soup base in the laboratory and reported significantly higher daily salt use if either they had suffered from infantile vomiting or diarrhea themselves or their mothers had suffered from morning sickness while pregnant with them (65).

Bitter

Detection and rejection of bitter are evident shortly after birth (49, 68, 69). Inborn responses have effects on initial acceptance of foods such as dark-green vegetables. We know less about how responses to bitter tastes can be modified during early life (but see below). In animal models, lack of early exposure to bitterness affects taste system development. In rodents, early taste deprivation remodels the central nervous system (70), whereas experience with bitterness during early life changes bitter taste preferences in adulthood (71).

Much recent research has focused on understanding how polymorphisms in the genes that encode taste receptors result in differential taste patterns in humans, beginning in childhood (age ~3 y onward). Of the 25 bitter taste receptors recently discovered (see reference 72 for review), TAS2R38 is the most studied. Genetic variation in this receptor translates into individual differences in taste sensitivity for phenylthiocarbamide, the related chemical propylthiouracil (PROP), and goitron found in cruciferous vegetables such as broccoli (73). Although some individuals can detect these bitter-tasting compounds at low concentrations, others need much higher concentrations to detect them at all, due in part to polymorphisms on the TAS2R38 gene (73).

Psychophysical studies have shown that PROP sensitivity varies with age (58, 74, 75). Children heterozygous for these variants (AVI/PAV) perceived a bitter taste at lower PROP concentrations than did heterozygous adults, with intermediate thresholds for heterozygous adolescents. These results imply that bitter sensitivity can change over the life span. How these variations contribute to individual differences are important areas for future research.

EFFECTS OF EARLY TASTE EXPERIENCES: FIRST FOODS, AMNIOTIC FLUID, AND MOTHER’S MILK

Beginning early in life, we learn the rules of cuisine—how, when, and what to eat. Thus, it is not surprising that preferences for salt, sweet, and bitter can be modified early through repeated exposure to flavors in amniotic fluid, mother’s milk, formula, and solid foods. These experiences help infants develop preferences in later life for foods containing these flavors.

Evidence of developmental plasticity: sweet and salt

Through familiarization, children develop a sense of what should, or should not, taste sweet (56, 76, 77). Children routinely fed sugar water during infancy preferred sweeter liquids than did children who were rarely exposed (78). Children repeatedly exposed to a sweetened orange-flavored beverage for 8 consecutive days during their daily midmorning snack at school not only gave higher preference rankings for the beverage but also drank more of it at the end of the exposure period (79).

Most foods and beverages manufactured for pediatric populations are very high in both refined sugars or salt or both (80, 81). Research has shown that adding sugar to beverages (56) and to solid foods such as spaghetti, ricotta, and jicama (82) increases both liking and acceptance by young children. But 16% of children’s total caloric intake now comes from added sugars (83). In addition, our food supply now includes several low- or no-calorie sweeteners that provide sweetness with fewer calories (84), yet we know little of their impact on children’s acceptance, growth, and eating patterns (85). We also do not know the long-term consequences of children associating sweet taste with foods that are not inherently sweet (eg, yogurts, breakfast cereals, sandwich breads).

Like experiences with sweet, preferences for salt taste are shaped by experiences with foods during the first year of life. Consumption of moderate and strong salt solutions (86) or salty cereals (87) by infants <6 mo of age can modify their dietary patterns once they start eating table foods. In a prospective study in 61 infants, those exposed to starchy table foods (eg, grain products, biscuits), a significant source of sodium in infants’ diets, were significantly more likely to prefer a salty solution during infancy, and had a greater affinity for salty foods as preschoolers, compared with children fed lower amounts of salt (86). Thus, early experiences modulate hedonic responses to these basic stimuli.

Salt is a critical part of the diet and also a key food preservative (88); thus, it is not surprising that we have evolved a strong desire to consume salt (47). However, it is now widely recognized that the average American consumes excess sodium chloride. The recent Dietary Guidelines for Americans report (89) recommends a maximum sodium intake of 2300 mg/d for healthy adults and 1500 mg/d for many subpopulations that together make up >50% of the total population; sodium intake is well above adequate amounts of 1000 mg/d at 1–3 y and 1200 mg/d at 4–8 y (90).

In adults, the vast majority of salt consumption comes from manufactured foods or prepared food at restaurants (91). Thus, consumers have relatively little control over or even knowledge of how much salt they consume. A recent Institute of Medicine report (92) stressed the importance of understanding salt taste and salt taste preference in children and how early experiences modulate these sensory responses. Salt in the food environment of infants and children—and any changes in lowering the overall amounts—may “have the most profound effects” (92). And the same may be true for sugar.

The first foods: amniotic fluid and mother’s milk

Relatively little attention has been paid to how humans learn to like the flavors of foods. During the past 2 decades, we have systematically investigated the transfer of flavors (dietary volatiles) to amniotic fluid and human breast milk to determine their effects on behaviors of breastfed infants (see reference 30 for review). A wide variety of flavors either ingested (eg, fruit, vegetables, spices) or inhaled (eg, tobacco, perfumes) by the mother are transmitted to her amniotic fluid and/or milk, significantly increasing in intensity in milk within hours after consumption. Infants’ experience with these volatiles and tastes modifies their acceptance in mother’s milk, formula, and solid foods.

For weaning, developmental processes must ensure that young mammals learn both what to eat and how to forage (30, 93). In a wide variety of species, they first learn about their mothers’
dietary choices through transmitted flavor cues (see reference 30 for review), which cause neurologic and physiologic changes that influence later behaviors. In a recent study, nursing young mice exposed to retronasally perceived odors (flavors) that activated specific olfactory receptors on sensory neurons had significantly larger glomeruli and significant preferences for the flavor compared with unexposed mice (94). Thus, early experiences with flavors in milk can result in enhanced detection of these learned odors later in life, which in nature would facilitate selection of foods with these odors.

There is also evidence, as reviewed above, that dietary learning in humans is more pronounced during early life. In the first randomized clinical study of development of flavor preferences, we assigned groups of pregnant women to drink carrot juice during the last trimester of pregnancy or during the first 3 mo of lactation, or to avoid carrots and carrot juice during both pregnancy and lactation. When mothers weaned their infants at ~6 mo of age, infants exposed to carrot flavors in either amniotic fluid or mother’s milk ate more of carrot-flavored cereal and made fewer faces of distaste than did nonexposed infants.

This continuity in flavor helps the infant transition to solid foods—for example, breastfed infants are more accepting of cereal prepared with mother’s milk than cereal prepared with water (95). Breastfeeding confers greater acceptance of healthy foods (eg, fruit, vegetables) only if they are part of the mothers’ diet (28, 96). Mothers typically feed children foods that are part of their own diet and culture, so the breastfeeding infant is learning about foods his or she will be offered. The sensory experiences with food flavors in mother’s milk in children whose mothers eat a varied diet may explain why children who were breastfed tend to be less picky (97) and more willing to try new foods during childhood (41, 42).

**Formula**

In striking contrast to the varied and rich sensory experiences of breastfed infants, early flavor experience of formula-fed infants is more monotone and lacks the volatiles of the foods of the mother’s diet. In addition, there are striking differences in flavors among the different types of formulas [eg, cow milk, soy, partial hydrolysate, extensive protein hydrolysate formula (ePHF)] and brands of formulas, and formula-fed infants learn to prefer the flavors of the formula they are fed and foods containing these flavors (13, 26, 29, 98–102).

For example, the distinctive flavor of ePHF is partly a result of abundant free amino acids, most notably glutamate (105), a key compound triggering the “umami” or savory taste quality that occurs naturally in many foods, such as broths. ePHF also contains aromatics (eg, sulfur volatiles) that are also found in cruciferous vegetables, such as broccoli. Infants fed ePHF ate more of infant cereals that tasted savory, sour, and bitter; ate them at a faster rate; and showed fewer facial expressions of distaste during feeding than did infants fed milk-based formulas (102). Both breastfed and ePHF-fed infants showed more positive facial reactions to savory formula, perhaps because breast milk (103) and ePHF (105) are both high in glutamate.

Research has also shown that how long infants are fed a type of formula affects their earliest responses to savory food (27, 102). In a randomized controlled study, infants fed ePHF for 3 or 8 mo, but not for 1 mo, showed greater acceptance of a savory broth relative to a plain broth and consumed it at a faster rate (27). The effects of early exposure appear to be particularly persistent and lead to heightened preferences for foods that contain volatiles also found in ePHF, such as broccoli, several years after the last formula exposure (101).

These findings have important implications for future research. Just as breastfed infants each experience a unique flavor palette through their mother’s breast milk, formula-fed infants are exposed to different aromas and tastes depending on the type and brand of formula used. In addition, how and whether the infant learns to like the flavor depend on the timing and duration of exposure (see also references 37 and 40). Perhaps most important, unlike breastfed infants, formula-fed infants may be attracted to flavors that may not be among the foods the family eats. Foods disliked by mothers typically are not offered to children (31); thus, for example, if mothers feed ePHF to their infants but never eat broccoli themselves, the likelihood that their infants will express and solidify their preferences for this vegetable is markedly diminished.

We should emphasize that early milk feedings are typically not either breast milk or formula but rather a combination of the 2, with most infants feeding formula when they begin to experience complementary foods (104). Future research should define both breastfeeding and formula feeding in terms of duration and exclusivity, as well as type and brand of formula, because formulas differ profoundly in composition and flavor profiles and have differential effects on flavor preferences (26, 27, 101, 102) and growth trajectories (105) during the first year of life (see reference 13 for previous review).

**EVIDENCE-BASED STRATEGIES ON FRUIT AND VEGETABLE ACCEPTANCE DURING INFANCY**

Basic research provides insights into the role of repeated exposure and variety in how infants learn to like fruit and vegetables. During the first year of life, infants make the dramatic transition from an exclusive liquid diet to a mixed diet consisting of breast milk or formula and a variety of complementary foods, and likely encounter a wide range of flavors and textures.

Concerns about how to wean children (eg, what types of foods to introduce, in what order) represent one of the primary matters mothers discuss with pediatricians. Because of the lack of research, many feeding practices are based on idiosyncratic parental behavior, family traditions, or medical lore. One example of such lore relates that infants should not have any previous experience with fruit before they are introduced to green vegetables because their inherent sweet preferences will interfere with acceptance of foods that taste bitter. However, no data support this contention, and in fact, one study showed no difference in carrot acceptance by infants with or without previous exposure to fruit (106).

Regardless of early feeding experiences, infants weaned to complementary foods learn through both repeated exposure (8–10 exposures) to a particular food and exposure to foods that vary in both flavor and texture—this, in turn, promotes willingness to eat not only introduced foods but also other, novel foods (82, 96, 106–111) (see Table 1). Exposing infants to multiple sensory contrasts (between- and within-meal flavor variety) also provides more opportunities to develop conditioned flavor preferences based on the postigestive reinforcing effects of nutritious foods (107). Feeding a novel food along with a familiar food might be an optimal combination to progressively accustom
<table>
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<td>Pears</td>
<td>Increased acceptance of pears; no effect on acceptance of novel vegetable (green beans)</td>
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<td>Peas, potatoes, squash</td>
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<td>Increased acceptance of diced apples in those who experienced more complex textures</td>
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<td><strong>Between- plus within-meal variety</strong></td>
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<td>8 d</td>
<td>Squash/peas, carrot/peas, squash/spinach</td>
<td>Increased acceptance of carrots and spinach; increased acceptance of novel vegetable (green beans)</td>
<td>Mennella et al, 2008 (107)</td>
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1 Infant was fed one target food at the same time of day for a number of days.
2 This study included both infants and toddlers.
3 Infant was fed only one target food each day, and the type of target food was alternated daily.
4 Infant was fed 2 target foods each day, and the pairs of foods varied from day to day.
CONCLUDING REMARKS

Textures may also be important. For example, 6- to 12-mo-old infants may continue to show facial expressions of distaste (eg, grimace), even though they are increasing their intake of a food with repeated exposure. Therefore, caregivers should focus on the infants’ willingness to eat the food and not just the facial expressions made during feeding. Ultimately, the goal is to gradually accustom children to a varied diet that meets nutritional needs for growth and development and provides them with opportunities to learn to like and prefer a variety of healthy foods.

Another important component of foods is their texture. This area has received scant scientific attention. Nevertheless, there is some evidence to suggest that the timing of exposure to varied textures may also be important. For example, 6- to 12-mo-old infants who experienced a variety of different-textured applesauce (eg, puréed, lumpy, diced) preferred greater texture complexity when tested later (109). Also, 7-y-old children who were introduced to lumpy solids after 9 mo of age, compared with between 6 and 9 mo of age, ate less of many food groups, including all 10 categories of fruit and vegetables, and were reported as having significantly more feeding problems (109). Further research is needed to examine, for example, whether there is a sensitive period during which lack of exposure to a variety of textures and flavors hinders acceptance of such foods in the long term. Likewise, what are the long-term consequences of mothers who eat a “junk food” diet during pregnancy and lactation. Emerging animal research models have shown that high maternal intakes of sugars and fats during pregnancy and lactation result in altered development of the central reward system in offspring and excessive junk-food intake in postnatal life (112, 113).

CONCLUDING REMARKS

Many of the chronic illnesses that plague modern society, such as obesity, diabetes, and hypertension, derive in large part from poor food choices, which relate to food and flavor experiences early in life. Although most people view food choice as a cultural trait, not directly related to our biology (114), overwhelming evidence suggests that children’s biology makes them especially vulnerable to the current food environment of processed foods high in salt and refined sugars. Thus, the struggle parents have in modifying their children’s diets to reduce added sugars and salt appears to have a strong biological basis, emphasizing the need for new strategies to approach children’s diets.

Although we cannot easily change children’s innate liking of sweets and salts and disliking of bitterness—we cannot get them to prefer broccoli to candy—our growing knowledge of how, beginning very early in life, sensory experience can shape and modify flavor and food preferences can help us direct children’s preferences more toward healthy flavors and variety and less toward excess sweet and salty tastes. Because arrays of dietary flavors are transmitted from the maternal diet to both amniotic fluid and mother’s milk, mothers can get their infants off to a good start by eating a diet rich in healthy foods, both while they are pregnant and while they breastfeed. Whereas infants fed formula may initially be less accepting of some fruit and vegetables that are not similar to the flavors of their formulas, they, too, can learn to like these foods: once weaned, both breastfed and formula-fed infants learn to accept foods through repeated exposure and dietary variety. However, it is important to emphasize that such foods need to be part of the family’s diet so that once the preference develops, the infant continues to be exposed to the food to maintain the preference, learning to like more complicated flavors and textures. Investigating whether there are optimum periods when experience promotes greater liking will go a long way toward promoting healthy eating and, in turn, addressing the many illnesses related to poor food choices.

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