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**Disclosure Statement Guest Editors**

J. Bhatia serves on the Editorial Board of *Annales Nestlé* and on the Executive Committee of the Nestlé Nutrition Institute. He has been a speaker for Mead Johnson Nutrition and Nestlé Nutrition Institute. M. Makrides served on the scientific advisory board of the Nestlé Nutrition Institute and currently serves on the scientific advisory board of Fonterra.

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The Nestlé Nutrition Institute was created to provide health professionals with up-to-date information on nutrition and nutrition-related disorders in order to enable them to continuously improve patient care based on the latest medical and scientific developments.

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*Natalia Wagemans, MD*
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We are witnessing a worldwide epidemic of obesity in children, adolescents, and adults. While obesity is multifactorial in origin, the increased prevalence of obesity has been paralleled by an increased consumption of “sweet” in the form of refined sugars and fat. In nature, sweetness can be equated to energy and is associated with a powerful hedonic appeal which is observed across individuals of all ages, races, and cultures. Given that in its simplest form, increased weight gain occurs when energy intake exceeds energy consumption, one factor that is possibly modifiable is the preference of sweets and perhaps a lifelong modification towards a healthier eating lifestyle.

In this context, this issue explores the development of sensory preferences spanning the period from the fetus to childhood. Dr. Alison Ventura examines the association between breast- and formula-feeding and taste preferences, and how infants’ preferences develop during the introduction of complementary foods and beverages. Globally, as she states, “a growing body of epidemiological studies suggest that the early effects of breastfeeding on acceptance of and preference for healthy foods may translate into healthier dietary patterns during later life.” As we promote and practice breastfeeding, modifying the quantity and quality of complementary foods and beyond may also help shape future eating habits.

The next chapter explores flavor perception and preference development in human infants. Dr. Catherine Forestell reiterates that children are born with a biological predisposition to prefer sweet and to avoid bitter foods such as green leafy vegetables. The attraction to energy-dense foods may have enhanced survival in food-scarce environments, but it is maladaptive in most of the world today. The flavors from the mother’s diet are transmitted to amniotic fluid and breast milk. Further, repeated exposures to a variety of foods are required to promote the infant’s willingness to consume novel foods. Dr. Forestell also examines why children prefer or dislike certain foods and ways to shift their inborn preferences through early sensory experiences. A mother’s healthy diet increases the likelihood that her child will prefer the same healthy foods. A family’s decision to purchase healthy foods and shaping dietary habits would be one more step towards decreasing energy consumption.

Dr. Matthew Kochem then reviews the contribution of type 1 taste receptors (T1Rs), which are responsible for sweet and umami taste, to intestinal glucose absorption, blood sugar and insulin regulation, and most importantly, the body’s responses to excessive energy intake. These T1Rs are expressed in non-oral tissues and guide the consumption of sweet and savory foods. In mice lacking these receptors, there appears to be partial protection against diet-induced obesity and hyperinsulinemia. T1Rs were highly adaptive for human ancestors who needed to “quickly evaluate the nutritive value of foods and efficiently store fuel.” In modern times, with sufficiency of energy and in obesogenic environments, modification of...
these receptors, rather than overstimulation, may be beneficial to long-term health, and further research is needed to explore these relationships.

Dr. Robert Murray expands further on the first 1,000 days where the timing, amount, and nutritional quality of complementary foods and beverages not only provides for the physical growth of the child but also its brain. As the other contributors have stated, sweetness is a central component of the feeding experiences of the fetus, infant, and child. Natural and added sugars are a substantial portion of the daily intake, and research suggests that early food preferences track over the life span raising the question that early diet influences the onset of obesity as part of a multifactorial etiological basis. Dr. Murray too reiterates the hedonistic effect of sweetened foods and ends with the suggestion that other flavor components as well as natural and added sugars in combination may be a way to enhance diet quality and lay a strong foundation for life-long nutrition.

We thank Natalia Wagemans and José Saavedra from Nestlé Nutrition Institute for their support of this supplement issue of Annals of Nutrition and Metabolism as it brings to light the influence of flavors, the acquisition of taste preferences, and early nutritional experiences, including fetal and neonatal, in the establishment of eating behavior.

Jatinder Bhatia
Maria Makrides
A major developmental task during the first years of life is for the child to learn both how and what to eat, as well as to develop preferences for a wide array of healthy foods.

**Key insights**

The first 1,000 days of life – between conception and 2 years of age – are a key window of time during which an infant’s flavor and food preferences develop. Maturation of smell and taste is a continuum that begins during fetal development and lasts throughout the life-course. Although human innate taste preferences are driven by an attraction to sweet and salty tastes, amniotic fluid and breastmilk provide the vehicle through which infants can learn to prefer the tastes and flavors of different foods.

**Current knowledge**

Research on infants’ flavor and food preferences during the weaning period has identified 3 mechanisms by which preferences emerge: repeated exposure, variety exposure, and associative conditioning. Infants who are repeatedly exposed to a novel food show increased intake and positive behavioral responses to that food. However, infants who are repeatedly exposed to a variety of foods show increased acceptance of the foods to which they are exposed, as well as to other novel foods. Finally, infants show greater acceptance of a novel food when it is paired with a familiar, preferred flavor or food. These 3 key components of preference development characterize the experience afforded by human milk.

**Practical implications**

Rapid weight gain during infancy is one of the earliest risk factors for the development of obesity and metabolic disease in later life. The first 1,000 days are therefore a critical window for targeting obesity prevention efforts. Breastfed children have a head start in developing preferences for a wider variety of healthy foods compared to formula-fed children. Breastfeeding exposes infants to a spectrum of novel flavors that are paired with the familiar flavors already contained in milk, leading children to be more accepting of different foods during weaning. Encouraging breastfeeding and healthy diets in pregnant and lactating women is key towards building the foundation for healthy eating in the next generation.

**Recommended reading**

Does Breastfeeding Shape Food Preferences? Links to Obesity

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Key Messages
• The first 2 years of life are a critical window for the development of flavor and food preferences.
• The flavors of the mothers’ diet are transmitted through the amniotic fluid and breast milk, and young infants develop preferences for flavors to which they are repeatedly exposed within familiar contexts.
• Breastfeeding plays a role in promoting infants’ acceptance of and preference for healthy foods during weaning, which is an important foundation for efforts to promote healthier dietary intakes and growth trajectories during childhood.

Keywords
Breastfeeding · Food preferences · Flavor preferences · Formula feeding · Obesity · Infant

Abstract
The first 2 years of life have been recognized as a critical window for obesity prevention efforts. This period is characterized by rapid growth and development and, in a relatively short period of time, a child transitions from a purely milk-based diet to a more varied solid-food diet. Much learning about food and eating occurs during this critical window, and it is well-documented that early feeding and dietary exposures predict later food preferences, eating behaviors, and dietary patterns. The focus of this review will be on the earliest feeding experiences – breast- and formula-feeding – and the unique role of breastfeeding in shaping children’s food preferences. Epidemiological data illustrate that children who were breastfed have healthier dietary patterns compared to children who were formula-fed, even after controlling for relevant sociodemographic characteristics associated with healthier dietary and lifestyle patterns. These dietary differences are underlined, in part, by early differences in the opportunities for flavor learning and preference development afforded by breast- versus formula-feeding. In particular, the flavors of the mothers’ diet are transmitted from mother to child through the amniotic fluid and breastmilk. The flavors experienced in these mediums shape later food preferences and acceptance of the solid foods of the family and culture onto which the infant is weaned. All infants learn from flavor experiences in utero, but only breastfed infants receive the additional reinforcement and flavor learning provided by continued repeated exposure to a wide variety of flavors that occurs during breastfeeding. Given the numerous benefits of breastfeeding, promotion of breastfeeding during early infancy is an important focus for primary prevention efforts and should be combined with efforts to ensure that mothers consume healthy, varied diets during pregnancy and lactation, and expose their infants to a wide array of foods during weaning and solid-food feeding.
Introduction

The American Academy of Pediatrics recommends infants be exclusively breastfed for about the first 6 months, followed by the introduction of complementary foods and beverages, and continued breastfeeding through at least the first year [1]. This recommendation reflects that the first year of life is characterized by rapid growth and development during which infants transition from a purely milk-based diet to a more varied solid-food diet over a relatively short period of time [2]. Dietary patterns emerge during this period and track from infancy into later childhood [3] and adulthood [4], and it is widely recommended that both children and adults consume diets high in fruits, vegetables, whole grains, low-fat dairy, and lean protein sources, and low in added sugar, saturated fats, and sodium [5].

Many families are not meeting recommendations for early feeding practices and dietary patterns. Eighty-one percent of mothers initiate breastfeeding at birth, but only 22% of infants are exclusively breastfed through 6 months of age [6]. An additional 30% of infants are fed a mix of breast milk and formula by 6 months, with the remaining 48% of 6-month-old infants exclusively formula-fed [6]. Adherence to recommendations does not improve once infants are fed a predominantly solid-food diet. Data from the Feeding Infants and Toddlers Study (FITS) illustrate that 26% of young children fail to consume at least 1 serving of fruit on a given day and 28% do not consume at least 1 serving of vegetables [7]. Only 11–24% of young children consume at least 1 serving of nutrient-dense, dark green or deep yellow vegetables per day. In contrast, over 30% of young children consume white or fried potatoes daily, and 63% consume at least 1 serving of desserts, sweets, or sweetened beverages daily. These dietary patterns continue to worsen throughout later childhood and adolescence [7, 8].

Given the importance of high-quality, nutrient-dense diets for promoting healthy developmental and cardiometabolic outcomes, improvement of young children’s dietary patterns is a critical focus for health promotion and primary prevention efforts. Parents and caregivers are largely in charge of which foods are offered to young children, but children’s food preferences are a major driver of the types of foods offered, as well as the types of foods that are actually consumed. Thus, the focus of this review will be on how these preferences develop during infancy to highlight possible targets for health promotion efforts. As will be discussed below, young children’s preferences are initially hedonically driven, but can be shaped by early exposures and experiences. This review will focus on the earliest feeding experiences – breast- and formula-feeding – and the unique role of breastfeeding in shaping children’s food preferences.

Preference Development during the Prenatal Period

The development of sensory preferences begins in utero; gustatory and olfactory systems emerge during the first trimester and these systems achieve functional maturity by the end of gestation [9]. The functional capacity of these systems in utero provides the opportunity for early sensory learning that prepares the fetus to be attracted to tastes, flavors, and foods that are safe, will promote growth, and are available within the postnatal environment.

It is well-established that gustatory and olfactory stimuli are transferred from mother to fetus through the amniotic fluid [10], and this experience is an initial step in the development of later flavor and food preferences. The fetus can detect chemosensory stimuli present in the amniotic fluid, and repeated exposure to these stimuli influences neonates’ later behavioral responses to those same stimuli. For example, during the first few days after birth, neonates show preference for the odor of their own mother’s amniotic fluid when compared to the odor of distilled water [11] or the amniotic fluid of another parturient mother [12]. Additionally, mothers who regularly consumed garlic [13] or anise [14] during the third trimester of pregnancy had neonates who showed greater preference for the odor of garlic or anise, respectively, compared to neonates of mothers who did not regularly consume those foods. Experimental work has illustrated that prenatal exposure to carrot flavor leads infants to prefer carrot-flavored to plain cereal during weaning, indicating that prenatal exposures impact later food preferences [15].

An early benefit of prenatal sensory learning was demonstrated in a series of studies by Marlier and colleagues [12, 16]. They noted that 2-day-old newborns could not discriminate between the odor of their mothers’ amniotic fluid and colostrum, which suggests continuity exists for the chemosensory properties of amniotic and lacteal fluids [12]. This continuity likely supports the infant’s attraction to breast milk as a nutrient source in the early postpartum period. By day 4, infants showed a preference for the odor of their mothers’ transitional milk over the odor of their mothers’ amniotic fluid, likely due to the repeated exposure to the lacteal fluids and changing properties of these fluids as they transition from colostrum to...
mature breast milk [12]. In contrast, infants who were formula-fed at birth showed preference for the odor of their mothers’ amniotic fluid compared to the odor of the formula they were fed, and this preference persisted through the first 4 days postpartum [16]. Four-day-old newborns showed clear preferences for the odor of human milk (whether from their own mother or not) compared to formula [17]. Thus, neonates prefer stimuli of biological origins and significance (e.g., breast milk) to those of synthetic origin or without immediate biological significance (e.g., synthetic milk).

Preference Development during the Postnatal Period

At birth, infants exhibit innate preferences for sweet and savory and aversion to bitter and sour [18]; a preference for salt emerges around 4 months [19]. These innate taste preferences are thought to be adaptive, ensuring the infant is attracted to the initial food that will sustain growth (breast milk, which is high in lactose, a source of sweet taste, and free amino acid glutamate, a source of savory taste). Given that poisons are bitter and rancid foods are sour, these taste preferences also ensure that infants are less willing to consume foods that may induce harm.

Consideration of these initial preferences provide some insight into why many children eat diets that are high in desserts, sweets, sweetened beverages, and fried potatoes, and low in nutrient-dense, dark green and other vegetables: these are the diets to which they are innately attracted and readily prefer. However, infants exhibit high levels of plasticity and are responsive to the food-related stimuli to which they are exposed and the social cues that surround food and eating. Thus, a major developmental task during the first years of life is for the child to learn both how and what to eat, as well as to develop preferences for a wide array of healthy foods.

Flavors in breast milk and/or formula are a primary postnatal influence on infants’ developing flavor and food preferences. Although formula brands differ in their sensory profiles, formulas provide a more monotonous experience relative to breast milk. In particular, breast milk is similar to the amniotic fluid in that a wide array of flavor compounds that are transferred to and detectable in human milk, including garlic [20], carrot [21], vanilla [22], tobacco [23], alcohol [24], and lipophilic flavor compounds with molecular structures and sensory properties similar to those found in fruits, vegetables, sweets, and spices [25]. The appearance of these compounds in breast milk peaks approximately 2–3 h after consumption and, in some cases, are detectable for up to 8 h after consumption [25]. Thus, breastfeeding is unique from formula feeding in that it provides a “flavor bridge” between the flavors to which the infant was exposed in the womb and the flavors of the foods to which the infant will eventually be exposed during weaning [26].

Experimental research examining how infants’ preferences develop during the introduction of complementary foods and beverages has illustrated 3 mechanisms by which preferences emerge: repeated exposure, variety exposure, and associative conditioning. At the most basic level, infants who are merely repeatedly exposed to a novel food show increased intake and positive behavioral responses (e.g., positive facial expressions) to that food [27]. However, infants who are repeatedly exposed to a variety of foods (e.g., a rotating schedule of peas, potatoes, squash) show increased acceptance of the foods to which they are exposed, as well as to novel foods [28]. Infants also show greater acceptance of a novel food when it is paired with a familiar, preferred flavor or food compared to when it is presented alone [27].

These key components of preference development – repeated exposure, variety exposure, and associative conditioning – characterize the experience afforded by human milk. Because the flavors of the mother’s diet are transmitted from mother to child through the milk, the infant is repeatedly exposed to a wide variety of flavors, and novel flavors are paired with the familiar sweetness and flavors already present within the milk. Given this experience, it is no surprise that a large body of research illustrates that infants are responsive to the flavors contained within human milk and these early experiences are associated with later preferences and dietary patterns.

In particular, the varied sensory properties of human milk influence infant behavior, but, in the short term, the way in which the flavor of the milk impacts infant behavior depends on whether the infant has had recent experience with the flavor. For example, when breastfeeding mothers were instructed to consume a bland,
Breastfeeding and Food Preferences

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low-garlic diet for 3 days prior to testing, their 4- to 6-month-old infants spent a significantly longer time attached to the nipple and showed an increased number of sucks during a test feeding that occurred 1.5–3 h after their mothers ingested a garlic capsule compared to a control group of infants whose mothers consumed a placebo capsule [20]. Thus, infants are attracted to and stimulated by novel flavors in the milk [15, 20, 29]. In contrast, when breastfeeding mothers consumed a target flavor (e.g., garlic [29], carrot [21], or caraway [30]) in the days prior to testing (i.e., their infants were repeatedly exposed to these flavors in the breast milk), their infants showed no preference for the flavor relative to a plain control during a test feeding, which may be a form of sensory-specific satiety [21, 29]. In contrast to these short-term studies, longer-term studies of both breast- and formula-fed infants illustrate that, during solid-food feeding, infants and young children show greater preferences for the flavors to which they have been exposed through the amniotic fluid [15], breast milk [15], or formula [31]. Effects of early experience on taste and flavor preferences has been shown to last until at least 10 years of age [32, 33].

Although infants learn from their early flavor exposures during milk feeding regardless of whether fed breast milk or formula, the exposure to a wide variety of flavors afforded by breastfeeding appears to be advantageous during later weaning. During the introduction of solid foods (when infants are 4–6 months of age), parents generally report that their infants react positively to the vast majority of foods to which they are introduced [34]. However, reactions to novel foods vary according to the taste of the food, with salted vegetables more accepted than plain vegetables [34] and fruits or sweeter vegetables more readily accepted than more bitter vegetables [35].

It has also been documented in some [30, 36], but not all [27, 34, 35], studies that breastfed infants are initially more accepting of novel foods and that repeated exposure to a novel food leads to greater increases in intake for breastfed compared to formula-fed infants. Similarly, breastfed infants exhibit a greater response to variety exposure than formula-fed infants [37], and the effect of variety exposure, either through breastfeeding or offering a variety of flavors, is still evident at 3 and 6 years of age [38]. During later childhood, children who were breastfed exhibit lower levels of neophobia (or fear of new foods) [39] and are less picky [40] compared to children who were formula-fed.

**Associations between Breastfeeding and Later Dietary Patterns**

Globally, a growing body of epidemiological studies suggest that the early effects of breastfeeding on acceptance of and preferences for healthy foods may translate into healthier dietary patterns during later life. For example, in a cohort of Australian children, longer breastfeeding durations were associated with intakes of greater varieties of healthy foods and greater varieties of fruits and vegetables when children were 2 years old, independent of family demographics [41]. In a recent analysis of 4 European cohorts of children aged 2–4 years living in the United Kingdom, France, Greece, and Portugal, longer breastfeeding durations predicted higher fruit and vegetable intakes during later childhood, even after adjusting for maternal intakes and relevant sociodemographic variables [42]. Similarly, a study of Canadian children illustrated that 4-year-old children who were exclusively breastfed for 3 or more months had significantly higher adjusted odds of consuming 2 or more servings of vegetables per day when compared to children who were formula-fed or partially breastfed [43]. Other studies of US, Brazilian, and Dutch cohorts have demonstrated similar associations between breastfeeding through the first year [44–46] and/or exclusive breastfeeding for ≥3 months [45, 47] and higher consumption of fruits and vegetables when children are 4–7 years old.

**Associations between Breastfeeding and Risk for Obesity**

The etiology of obesity is multifactorial with a number of important risk factors occurring prior to birth (Fig. 1) [48]. However, during the postnatal period, the first 2 years have been recognized as a critical period for development, especially as it relates to health outcomes and risk for obesity [49] and dietary patterns have been highlighted as important contributors to the development of obesity [50]. Given the evidence for effects of breastfeeding on early food preferences and associations between breastfeeding and later dietary patterns, it is plausible to...
consider promotion of breastfeeding as a component of obesity prevention efforts and examine possible effects of breastfeeding on later growth patterns and obesity risk. During early infancy, breastfeeding is associated with healthier growth patterns. Breastfed infants consume a lesser volume during each feeding and over the course of a day compared to formula-fed infants [51] and infants fed breast milk are significantly lighter by 9 months of age [52]. Breastfed infants also gain healthier amounts of weight during the first year postpartum and are less likely to show patterns of rapid weight gain during infancy compared to their formula-fed peers [53]. Excess weight gain among formula-fed infants is not offset by equally greater gains in length and appears to be attributable to higher levels of fat mass (as opposed to fat-free mass) in formula-fed infants [54].

Whether these early growth differences translate to later weight outcomes is unclear given somewhat equivocal findings for associations between breastfeeding and later risk for obesity. Some studies suggest that the effects of breastfeeding on promoting healthy weight gain trajectories and weight status are long lasting, extending into later childhood, adolescence, and adulthood, even after controlling for sociodemographic characteristics. Indeed, several meta-analyses of published research have consistently illustrated modest associations between breastfeeding (when compared to formula-feeding) and reduced risk of obesity later in life [55–60], as well as a significant dose-response effect of breastfeeding duration on reduced risk for later obesity [55, 59]. However, a recent cluster-randomized trial (the Promotion of Breastfeeding Intervention Trial [PROBIT]), within which mothers who initiated breastfeeding participated in a
breastfeeding promotion intervention or standard care, did not find differences in the prevalence of obesity for children of mothers in the intervention versus control groups, despite significant effects of the intervention on increasing the duration and exclusivity of breastfeeding [61, 62]. These findings may suggest that the links between breastfeeding and obesity are due to confounding factors, but this conclusion is limited by the fact that all mothers in this sample initiated breastfeeding and a comparison of outcomes for infants who were breastfed versus those who were exclusively formula-fed was not possible.

**Implications and Recommendations**

A child’s first 1,000 days – defined as the period from conception to the age of 2 years – are a critical period for obesity prevention efforts [49]. Although the etiology of obesity is complex, rapid weight gain during infancy has been highlighted as one of the earliest postnatal risk factors for the development of later obesity and metabolic dysfunction [63] and has been recognized as a prime target for prevention and intervention efforts [64]. Early feeding exposures are central when considering influences on risk for rapid weight gain and obesity, and it is well-documented that these early feeding and dietary exposures are significant predictors of later food preferences, eating behaviors, and dietary patterns.

Although breastfeeding is not a panacea, a large body of research illustrates that breastfeeding can facilitate the development of preferences for healthy foods during a critical period of development. Specifically, it appears that children who are breastfed get a “jump start” on developing preferences for a wide array of healthy foods when compared to children who are formula-fed, mainly because breastfeeding allows children to be repeatedly exposed to a wide array of novel flavors that are paired with the familiar flavors already contained within the milk. This experience may lead infants to be more accepting of foods during weaning, because they are already familiar with and have developed a preference for the flavors of these foods well before they experience them in solid-food form. Given the numerous benefits of breastfeeding, promotion of breastfeeding during early infancy is an important focus for primary prevention efforts and should be combined with efforts to ensure mothers consume healthy, varied diets during pregnancy and lactation and expose their infants to a wide array of healthy foods during weaning and complementary feeding.

**Disclosure Statement**

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**References**


Responses to basic tastes are remarkably similar across cultures and species, which suggests these responses are a product of children’s basic biology

Flavor Perception and Preference Development in Human Infants
by Catherine A. Forestell

Key insights
Children’s innate dietary preferences are a reflection of our basic biology, which drives the inclination towards sweet items and the avoidance of bitter-tasting items such as green leafy vegetables. Once essential for our survival, this adaptive mechanism is now at odds with an environment overloaded with unhealthy foods. Nevertheless, this biological predisposition can be overcome by modulating early flavor experiences during gestation, breastfeeding, and weaning.

Current knowledge
In comparison to other senses such as sight and sound, the sense of taste begins to emerge early. During the last trimester of pre-natal development, taste buds are already capable of detecting and transmitting information to the central nervous system. The intrauterine environment is rich in flavors that change according to the mother’s diet. The fetus actively swallows between 500 and 1,000 mL of amniotic fluid per day during the last trimester. After birth, the flavors from the maternal diet continue to be transmitted to the infant via breast milk. This ongoing exposure to flavors guides the infant’s taste preferences and sets the foundation for dietary choices made in later childhood.

Practical implications
Pregnant and nursing women should be encouraged to consume a healthy diet that includes a variety of flavors. Early exposure of the developing fetus or young infant to flavors associated with fruits and vegetables can shape food and flavor preferences, thereby increasing the infant’s acceptance of healthy foods in the environment. Repeated exposure to healthy foods at weaning will reinforce and expand these preferences.

Recommended reading
Abstract
As most parents and caregivers are aware, feeding children a nutritionally balanced diet can be challenging. Children are born with a biological predisposition to prefer sweet and to avoid bitter foods such as green leafy vegetables. It has been hypothesized that this predisposition evolved to attract children to energy-dense foods while discouraging the consumption of toxins. Although this may have enhanced survival in environments historically characterized by food scarcity, it is clearly maladaptive in many of today's food environments where children are surrounded by an abundance of sweet-tasting, unhealthful foods and beverages that place them at risk for excessive weight gain. Because overweight or obese children tend to become overweight or obese adults who are at risk for a range of cardiovascular diseases, it is of primary importance to develop effective evidence-based strategies to promote the development of healthy eating styles. Fortunately, accumulating evidence...
suggests that, starting before birth and continuing throughout development, there are repeated and varied opportunities for children to learn to enjoy the flavors of healthful foods. Because flavors are transmitted from the maternal diet to amniotic fluid and breast milk, mothers who consume a variety of healthful foods throughout pregnancy and lactation provide their infants with an opportunity to learn to like these flavors. This in turn eases the transition to healthful foods at weaning. In contrast, infants fed formula learn to prefer its invariant flavor profile, which differs from breast milk, and may initially be less accepting of flavors not found in formula. This process can continue throughout weaning and into childhood if infants are repeatedly exposed to a variety of healthful foods, even if they initially dislike them. These early-life sensory experiences establish food preferences and dietary patterns that set the stage for lifelong dietary habits.

### Introduction

Parents and caregivers face the ubiquitous challenge of providing their children with a balanced diet that promotes healthy growth and development. The USDA [1] recommends that families meet this challenge by feeding children a diverse, nutrient-dense diet that contains vegetables, fruits, whole grains, low-fat dairy products, and quality protein sources. As many parents lament, meeting these dietary recommendations is difficult for a number of reasons – not the least of which is that children tend to dislike vegetables and prefer sugar-sweetened foods and beverages. As a result, children generally avoid eating most vegetables and forgo consumption of natural sources of sugars such as fruit in favor of foods and beverages that are high in added sugars [2, 3]. This preference for simple sugars and energy-dense foods over nutrient-rich alternatives has dire health consequences. Children’s poor dietary habits are a risk factor for several diseases, including pediatric obesity, type 2 diabetes, and hypertension, which have traditionally afflicted older adults [4, 5].

**Children’s poor dietary habits are a risk factor for several diseases, including pediatric obesity, type 2 diabetes, and hypertension**

This article provides an understanding of why children prefer or dislike certain foods and how we can shift their inborn preferences through early sensory experience. It begins with a brief overview of the ontogeny of sweet and bitter taste perception, both of which have important functional significance in children’s consumption of healthful, bitter-tasting vegetables and unhealthful, sweet-tasting desserts and beverages. It then reviews how early flavor experiences interact with the plasticity of the chemosensory system to shift children’s preferences and acceptance of fruit and vegetables. In sum, this research shows that, although children are born with biological predispositions to prefer highly sweet-tasting foods and beverages over healthful, less sweet alternatives, their preferences can be altered by early experiences from gestation through weaning and do not necessarily determine lifelong dietary habits.

### Taste and Flavor Perception

Flavor is a powerful determinant of human consummatory behavior. Although in everyday language the terms flavor and taste are often used interchangeably, flavor refers to the integrated sensation that arises from the combined input of taste, chemosensation, and olfaction [6]. For example, when we consume an orange soda, sugars and citric acid come into contact with taste receptors throughout the oral cavity and the gut, which send messages to the brain that allow us to perceive the sweet and sour taste of this beverage. We also experience the bite of carbon dioxide, which activates trigeminal nerve fibers that innervate the nasal and oral cavity, triggering chemosensation. In addition, the citrus odor travels retronasally along the back of the nasopharynx toward the roof of the nasal cavity, reaching olfactory receptors located in the epithelium of the nasal cavity. Unlike the limited number of primary tastes, which consist of sweet, sour, bitter, savory, and salty, there are thousands of distinctive odors with separable sensations that allow us to experience a rich array of flavors.

Relative to other sensory capacities such as vision and audition, the sense of taste begins to emerge relatively early. Behavioral studies using a variety of techniques suggest that by the last trimester of prenatal development taste buds are capable of detecting and communicating information to central nervous system structures responsible for organizing and controlling affective behaviors (for a more extensive review see [7]). Similarly, the olfactory bulb and receptor cells are functional by the last trimester. Given the extensive prenatal development of the chemosensory system, it is not surprising that the newborn is sensitive and responsive to odor, taste, and flavor stimuli at birth.
Age-Related Changes in Response to Sweet and Bitter Taste

Accumulating research suggests that preferences for basic tastes are a major determinant of children’s food choices and acceptance patterns [8–11]. Over the past few decades, our understanding of children’s perception and preference for basic tastes has grown substantially (for a review see [7]). We now know that children live in their own sensory world, with their sensitivities and preferences for tastes changing throughout childhood. Responses to basic tastes are remarkably similar across cultures and species, which suggests these responses are a product of children’s basic biology.

**Sweet Taste**

In nature, most sugars (e.g., fructose, maltose, and sucrose) have a small molecular weight and are found primarily in plants. These sugars provide sources of glucose, a key source of energy. For infants, the sweet sugar lactose found in breast milk can also be metabolized to provide glucose energy. Indirect evidence from early studies of fetuses [12], together with findings from studies of premature infants, suggests that detection of sweet taste stimuli is possible during late gestation [13]. This early experience may prepare newborns to detect and accept the basic taste of sweet found in breast milk, which contributes to their survival.

Palatable tastes, such as sucrose, are thought to induce sensory pleasure, which elicits appetitive reactions. As shown in Figure 1, tasting 0.73 M sucrose elicits facial relaxation, sucking movements, and sometimes smiling in newborns, as first described by Steiner [14] and later by Rosenstein and Oster [15]. Consistent with this, research has repeatedly demonstrated that infants preferentially consume sweet-tasting solutions relative to water and can differentiate varying degrees of sweetness (0.05–0.30 M) and different kinds of sugars; sucrose, fructose, glucose, and lactose [16]. These findings converge with physiological findings; for example, administration of drops of aqueous sucrose (0.73 M) to the tongues of newborn infants produced greater relative left-side activation in both frontal and parietal regions of the brain, which is considered to be a reliable indicator of positive emotion [17].

Compared to adults, who on average prefer 0.44 M sucrose, 5- to 10-year-old children have a much sweeter tooth, preferring 0.54 M sucrose [18], almost double the concentration of most soft drinks [19]. The higher preference for sucrose observed throughout childhood may be related to rapid physical growth during this time [20]. This hypothesis is supported by evidence that adolescents with higher sweet preferences also have higher levels of a biomarker for bone growth than do those with lower sweet preferences [21]. Because this biomarker increases during growth spurts, age-related declines in preference for sweet taste may correspond with cessation of physical growth [22, 23].

**Bitter Taste**

In contrast to sweet taste, bitter taste appears to be disliked by infants at birth; as shown in Figure 1, they gape

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Fig. 1. Newborn’s orofacial responses to the sweet taste of 0.73 M sucrose (left) and the bitter taste of 0.003 M quinine (right) presented approximately 2 h after birth, before the first postnatal feed. Using a syringe, 0.2 mL of each taste solution at room temperature was presented to the central portion of the dorsal surface of the infant’s tongue. Reprinted with permission from [15].
when a bitter quinine solution (0.003 M) or urea solution (0.15–0.25 M) is placed on the tongue [14, 15]. However, intake studies reveal that newborns consume similar amounts of 0.18–0.48 M urea in water or in a weak sucrose solution compared to the diluent alone [24, 25]. Differential consumption of bitter urea solutions does not occur until infants are approximately 2 weeks of age [26] and is evidenced throughout childhood by a general avoidance of bitter-tasting foods. Together, the orofacial and consumption studies suggest that intake regulation of bitter solutions may mature postnatally.

Recent research in adults and children has focused on understanding the role genes play in individual differences in sensitivity to bitter tastes. Of the 25 human bitter taste receptor genes currently identified, TAS2R38 is the most commonly studied (for a review see [27]). Polymorphisms in the genes that encode this receptor determine much of the variation in taste sensitivity for a class of bitter-tasting chemicals that includes synthetic thiourea compounds (e.g., propylthiouracil [PROP]) and natural plant toxins (e.g., goitrin) found in cruciferous vegetables such as broccoli [28]. Due in part to polymorphisms on the TAS2R38 gene, some individuals have a high sensitivity threshold for this class of bitter tastes, while others have lower thresholds and as a result are more sensitive to the bitterness in cruciferous vegetables [29]. In addition to these individual differences, psychophysical studies have shown that PROP sensitivity appears to decrease with age. Children heterozygous for a TAS2R38 variant perceived lower concentrations of this bitter chemical than did heterozygous adolescents, who in turn detected lower concentrations than heterozygous adults [30, 31]. Such sensitivity to this class of bitter tastes may contribute to reduced acceptance of cruciferous vegetables during childhood.

Evolution, Today’s Obesogenic Environment, and Sensory Learning: A Bitter-Sweet Story

How do we explain children’s biological predispositions to prefer sweet-tasting and dislike bitter-tasting foods, even though they lead to maladaptive outcomes that threaten health? Looking back in our evolutionary history reveals that human’s current taste perceptions and preferences have been largely shaped by the ecological niches of our evolutionary ancestors. In order to adapt to specific environments that contain some types of food but not others, our sense of taste has changed and, by extension, so has our genome. Early hominoids used their sense of taste to identify nutritious food items among an expansive dietary repertoire. Preference for sweet tastes is thought to have evolved to attract us to energy-producing sugars that are important for growth and development.

However, eating can be dangerous – many risks are associated with making poor food selections, including the potentially lethal ingestion of harmful parasites, bacteria, and chemicals. As a result, rejection of bitter likely evolved to prevent ingestion of potentially dangerous substances, such as poisons, many of which we perceive as bitter. Although these biological predispositions were at one time adaptive, helping us select nutrients and avoid toxins, today preferences for sugary foods and avoidance of bitter vegetables do not provide an adaptive advantage in environments with easy access to a variety of palatable, energy-dense foods and safe fruits and vegetables.

Over the past century, significant changes in our food environment have occurred, including an increase in the number of fast food restaurants and availability of low-cost, energy-dense food options. These changes have been fueled by marketing strategies that target children’s inborn preferences for sweet taste [32]. Children can increase their preference for a food product after only a single exposure to a commercial, and this is strengthened with repeated exposures. In turn, these preferences affect their product purchase requests, which ultimately influence their parents’ purchasing decisions [33].

The marketing influence on children’s food preferences is of particular concern for a number of reasons. First, as discussed above, we do not need to encourage consumption of unhealthful foods, given that children are already predisposed to preferentially consume them. Not only are children attracted to the sweet taste of sugar in these foods, but the presence of sugar can also effectively suppress or mask the bitterness [34, 35] that is inherent in some foods and beverages (e.g., caffeinated energy drinks) that children would otherwise avoid.

Second, through familiarization with sweetened versions of foods and beverages that are not inherently sweet-tasting, such as yogurt, milk, or cereal, children develop an expectation that foods should taste sweet [36]. As a result of the intrinsic plasticity of the taste system, prefer-
ences for sweeter-tasting foods and beverages are readily acquired through early exposure to sweet taste. For example, longitudinal studies have shown that newborn infants who were regularly fed sugar water preferred significantly higher concentrations of sucrose solutions 2 years later compared to those who had no such experience [37]. Although correlational, these studies suggest that early dietary exposure to sweet foods is associated with later enhanced acceptance of sweet tastes. However, the opposite is also true: just as children’s preferences for sweet-tasting foods can be strengthened, preferences for healthful foods can increase as a result of early exposure to the flavors of these foods.

Accumulating evidence suggests that, starting before birth and continuing throughout development, repeated and varied opportunities to learn about the flavors of healthful foods increase later acceptance and consumption of these foods [38]. During fetal development, the intrauterine environment is rich in odor volatiles (i.e., flavors) that change as a function of the mothers’ diet. As discussed above, it is likely that the fetus is sensitive to and learning about this ever-changing flavor profile; by the last trimester the taste and olfactory receptors are functional, and the fetus is actively swallowing between 500 and 1,000 mL of amniotic fluid each day [39]. After birth, infants are exposed to a diet that is typically solely milk-based, consisting of breast milk, artificial milk (formula), or both. While the flavor of breast milk, like amniotic fluid, reflects the mother’s diet, the invariant flavor profile of formula does not (Fig. 2).

**Amniotic Fluid and Breast Milk**

A wide variety of flavors ingested by the mother are transmitted to amniotic fluid during pregnancy and to

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**Fig. 2.** Flavor experiences during pre- and postnatal development. Common flavors are initially experienced during the fetal period in utero, during postnatal feeding, and during weaning. After birth, the American Academy of Pediatrics recommends feeding only breast milk for the first 6 months of life, followed by a combination of solid foods and breast milk until the infant is at least 1 year old. This gradual transition to a diet consisting primarily of solid foods is represented by the gradated borders in the figure. Breast milk serves to bridge the flavor experiences during the fetal period to those at weaning (represented by solid black arrows). Many mothers choose to feed their infants formula exclusively, or to feed a combination of breast milk and formula (as represented by the dotted double arrow). In contrast to the varied sensory experiences of breast milk, the flavor of formula is monotone and lacks the volatiles of the foods of the mother’s diet. These experiences nevertheless affect infants’ acceptance of similar flavors at weaning (as represented by the solid grey arrow).
breast milk during lactation, including garlic [40], vanilla [41], anise [42], and carrot [43]. This ongoing exposure to the flavors within amniotic fluid and breast milk biases the infant’s flavor preferences for these foods. In one study, mothers consumed carrot juice either for 3 consecutive weeks during the last trimester of pregnancy, or during lactation, while those in a control group drank water during pregnancy and lactation and avoided carrots [43]. Infants exposed to the target flavor, either prenatally or postnatally, preferred carrot-flavored relative to plain cereal, whereas the control group showed no such preference. Further work in non-human animals has replicated these effects and has additionally shown that dogs exposed to aniseed throughout the perinatal period (i.e., pre- and postnatal exposure) displayed greater flavor preferences for aniseed at weaning than those exposed to aniseed either pre- or postnatally [44].

These results support the contention that the continuity of flavor experiences provided by breastfeeding helps with the transition to solid foods at weaning. This is further supported by findings that breastfed infants are more accepting of fruit than are formula-fed infants, but only if their mothers regularly ate this food during lactation [45]. Breastfed children may also be more willing to accept novel foods [46] and less picky as they grow older [47, 48], especially if their mothers eat a varied diet, which provides a more varied flavor profile in breast milk.

**Formula**

Infants who are exclusively formula-fed often receive just one type of formula, which limits their exposure to varied flavor experiences [49]. Despite the lack of flavor variety, different types and brands of formulas vary in their characteristic flavor profile, due to differences in their composition and processing [50]. For example, cow-milk-based formulas (CMFs) are described as having low levels of sweetness, with sour and cereal-like characteristics, whereas soy-protein-based formulas have sweet, sour, and bitter tastes. Extensively hydrolyzed protein formulas (ePHFs), the feeding regimen of choice for formula-fed infants who cannot tolerate intact proteins, have high levels of free amino acids, because its proteins are broken down by enzymes. These free amino acids impart a savory, bitter, and sour taste profile, as well as unpleasant odor volatiles (e.g., sulfur volatiles that are found in cruciferous vegetables, such as broccoli [51, 52]). Yet, infants fed ePHF early in life readily learn to accept its “off” flavors [53].

By taking advantage of the inherent differences in the flavor profiles among these formulas, researchers have shown that infants develop flavor preferences that reflect the type of formula they are fed. Compared to infants fed CMF, those fed ePHF ate more savory-, sour-, and bitter-tasting infant cereals at a faster rate and showed fewer facial expressions of distaste during feeding [54]. Moreover, ePHF-fed as well as breastfed infants were more likely to display positive facial reactions to savory-tasting cereal, perhaps because breast milk [55] and ePHF [56] are both high in the savory amino acid glutamate. Other research has shown that the length of time infants are fed ePHF influences their responses to savory food; those fed ePHF for at least 3 months showed greater acceptance of a savory broth relative to a plain broth [57]. Evidence shows that these early preferences can be long-lasting. Several years after the last formula exposure, children fed ePHF during infancy were more likely to prefer a sour-tasting apple juice than were children fed CMF [58]. They were also more likely to preferentially consume broccoli, which has flavor notes similar to ePHF [58]. In combination, these studies reveal that the tastes to which infants are exposed during formula feedings affect their acceptance of foods at weaning. However, if these flavors are not part of the family’s diet, infants may not reap the benefits of this early sensory learning. Rather, preferences for the foods that the family eats will be acquired at weaning through repeated exposure.

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**Children require 8–10 exposures to the taste of a food in order to increase acceptance of it**

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**Complementary Feeding: Increasing Preferences for Fruit and Vegetables**

At weaning, children transition from a milk-based to a mixed diet that consists of breast milk or formula and a variety of complementary foods. With the milk-based diet, infants learn to prefer foods through repeated exposure (with formula) or through exposure to a variety of flavors (with breast milk). The same is true for children at weaning: converging evidence from several experimental studies indicates that children require 8–10 exposures to the taste of a food in order to increase acceptance of it. It is important to note, however, that increased intake does not always coincide with increased liking [45]. Even when infants begin to consume more of a food after repeated exposure, they may continue to display negative facial responses (such as squinting) while eating it. Because these
negative orofacial responses persist after increased acceptance, parents are less likely to offer the food again [59]. To produce shifts in liking that mirror the changes in intake, exposure needs to continue beyond acceptance until liking occurs (i.e., when the infant begins to show fewer facial expressions of distaste) [45, 60].

Relative to merely repeating exposure to the same food, exposing infants to a variety of flavors has the added advantage of promoting infants’ willingness to consume novel foods. As shown in Figure 3, 8 days of exposure to a variety of vegetables increases acceptance of a novel-tasting vegetable [61, 62] but not of a novel fruit [61]. Similarly, 8 days of exposure to a variety of fruits increases acceptance of a novel fruit but not of a novel green vegetable [61]. It appears that the variety of foods presented must share some flavor characteristics of the novel food in order to increase its acceptance. More recent research has shown that exposure to flavor variety continues to be effective in increasing acceptance of fruit between 4 and 8 years of age [63]. However, this study did not find a similar increase in children’s preferences for vegetables, which suggests that shifting older children’s preference for vegetables may require other strategies such as associative conditioning [64].

It appears that additional factors may moderate the ease with which infants acquire flavor preferences for healthful foods, such as personal characteristics of the child. For example, children who were high in approach temperament were less likely to express facial expressions of distaste (i.e., gape) and consumed more of a bitter green vegetable [65]. Infants with approach temperaments may be more likely to try a greater variety of fruits and vegetables before the onset of neophobia at around 2 years of age. As discussed above, we are also gaining a better understanding of the molecular mechanisms underlying individual differences in taste sensitivity. For example, because of genotype differences, some individuals are more sensitive to the bitter taste of some vegetables and as a result may be less likely to eat these foods (e.g., [29, 66]). Yet another factor shown to be important is the parents’ feeding style. Osborne and Forestell [63] found that when children were exposed to a variety of fruits and vegetables, they were less likely to develop a preference for a novel fruit when their mothers reported pressuring them to eat. Thus, it appears that early and repeated sensory experiences, child temperament, taste receptor genotype, as well as the quality of mother-child interactions during feeding are just a few of the factors that interact to determine food preferences during childhood.

Final Remarks

While no single factor is responsible for the dramatic increases in overweight and obesity in the US over the past century, it is generally accepted that the consumption of sugar-sweetened products, especially beverages, is causally linked to increases in risk of chronic diseases, including type 2 diabetes, cardiovascular disease, hypertension, and stroke [67]. This is concerning because children are born with biological predispositions to preferentially consume sweet-tasting foods and beverages instead of other more healthful foods, such as green vegetables. Whether this early proclivity for sweet tastes leads to later unhealthy dietary habits depends in part on the child’s early sensory experiences. Health care providers should encourage pregnant and nursing women to consume healthful diets with a variety of flavors. Infants who are formula-fed should be exposed to a variety of flavors,
particularly those associated with fruits and vegetables, while the mother is pregnant and again at weaning. Although we cannot completely change children’s innate liking of sweets and disliking of bitterness, we have learned that early sensory experiences, which begin with the flavors of foods the mother eats during pregnancy and lactation, can shape and modify early flavor and food preferences, thereby increasing infants’ acceptance of the foods available in their environment. Thus, a mother’s healthy diet increases the likelihood that her child will prefer these same healthy foods. Repeated exposure to healthy foods at weaning will maintain and expand these preferences. Infants’ healthy dietary repertoire will continue to grow if they are exposed to a variety of healthy foods at weaning and throughout childhood.

To be sure, whether children have the opportunity to learn about healthful flavors early in life depends on many factors. A family’s decisions about food purchases and consumption are influenced by a range of socioenvironmental factors, such as culture, financial status, and education (e.g., [68]). An appreciation and a greater understanding of the complexity underlying food choices in families and how these affect the development of children’s food preferences will aid in the development of evidence-based strategies and programs to facilitate children’s early acceptance of fruit and vegetables.

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Our innate attraction to sweet-tasting foods, which served our ancestors in the tropical forests, has since become a public health concern.

Type 1 Taste Receptors in Taste and Metabolism

by Matthew Kochem

Key insights
Type 1 taste receptors (T1Rs) transduce sweet and savory tastes. Not only expressed on the tongue and mouth, T1Rs are also found in other metabolically active tissues throughout the body, such as the intestine and pancreas. These receptors convey the presence of sugars and amino acids, guiding food intake and regulating the metabolic response to foods.

Current knowledge
The consumption of a carbohydrate-rich meal causes a dramatic change in blood glucose levels. It is important to control large glucose fluctuations, since excessive amounts of glucose contribute to protein glycosylation and blood vessel damage. T1Rs may play a role in the post-oral absorption and metabolism of nutrients such as glucose. In the intestine and pancreas, T1Rs act as sensors that stimulate glucose absorption in the intestinal lumen and promote its clearance from the blood. Activation of T1Rs in the intestine is thought to stimulate the secretion of incretins (such as the hormone GLP-1) that in turn upregulate glucose transporter expression and potentiate glucose-stimulated insulin secretion.

Practical implications
GLP-1 is an incretin hormone that plays a central role in glucose-stimulated insulin secretion in the pancreas. GLP-1 is an attractive candidate for the treatment of type 2 diabetes mellitus (T2DM). GLP-1 receptor mimetic drugs such as liraglutide and exenatide are currently used for the treatment of T2DM. The emerging role of T1Rs in glucose regulation has also raised interest in the metabolic effects of sweeteners in the diet. However, it is still unclear whether T1Rs affect insulin secretion, glucose clearance, or both. Because these receptors facilitate nutrient consumption and absorption, T1R inhibition may in fact be beneficial in obesogenic environments. In vivo studies suggest that the absence of T1R may be beneficial in an obesogenic environment; T1R knockout mice were less likely to become obese when fed a high-fat diet. Although more research is needed, inhibition of T1Rs may therefore present an alternative strategy for the prevention of diabetes.

Recommended reading
Type 1 Taste Receptors in Taste and Metabolism

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Key Messages
- Type 1 taste receptors (T1Rs) guide the consumption of sweet and savory foods.
- T1Rs are expressed in non-oral tissues, where they are thought to stimulate absorptive and hormonal responses to ingested foods.
- Mice lacking T1Rs are partially protected against diet-induced obesity and hyperinsulinemia.
- Further research is needed to determine the effects of T1R activity on human health.

Keywords
Taste receptor · T1R · Sweet · Savory · Umami · Taste · Perception · Glycemia · Insulin · Obesity

Abstract
Our sense of taste allows us to evaluate the nutritive value of foods prior to ingesting them. Sweet taste signals the presence of sugars, and savory taste signals the presence of amino acids. The ability to identify these macronutrients in foods was likely crucial for the survival of our species when nourishing food sources were sparse. In modern, industrialized settings, taste perception continues to play an important role in human health as we attempt to prevent and treat conditions stemming from overnutrition. Recent research has revealed that type 1 taste receptors (T1Rs), which are largely responsible for sweet and umami taste, may also influence the absorption and metabolism of the foods we eat. Preliminary research shows that T1Rs contribute to intestinal glucose absorption, blood sugar and insulin regulation, and the body’s responses to excessive energy intake. In light of these findings, T1Rs have come to be understood as nutrient sensors, among other roles, that facilitate the selection, digestion, and metabolism of foods.

Introduction
Type 1 taste receptors (T1Rs) in the mouth signal the presence of saccharides and amino acids [1, 2]. The ability to detect these nutrients underlies a critical set of psychological and physiological processes that ensure human survival. T1Rs are largely responsible for the conscious perception of the appetitive sweet and umami tastes, which guide food intake [3]. Taste receptors may also regulate metabolic processes which promote efficient digestion and assimilation of the foods we eat.

Taste perception allows us to evaluate the chemical makeup of foods in order to determine whether they contain nutrients and/or toxins. Savory (umami) taste perception, primarily stimulated by glutamate and ribonucleotides, guides the consumption of protein sources.
This helps to ensure the consumption of essential amino acids, which cannot be synthesized by the body and must be obtained in the diet. Similarly, sweet taste perception guides the intake of carbohydrate, a critical energy source for the brain and other tissues. Considering the energy demands of growth, it is unsurprising that infants and children are innately and strongly attracted to sweet-tasting compounds [4].

Taste receptors are also implicated in the regulation of nutrient metabolism. Recent research shows that taste receptors are expressed not only in the oral cavity, but in metabolically active tissues throughout the body [5–13]. The majority of this work has focused on the roles of intestinal and pancreatic T1Rs in glucose metabolism. Data from in vitro and animal studies suggest that taste receptors in the intestine and pancreas facilitate glucose absorption and disposal [5, 14, 15]. Animals lacking T1Rs display dramatically altered responses to food ingestion and respond differently to obesogenic diets.

Because they participate in a host of processes involved in the consumption and metabolism of foods, taste receptors may play a key part in our understanding of nutrition-related diseases. This review will discuss the basic functions of T1Rs, the importance of sweet and savory taste, and the striking effects of taste receptors on metabolism and long-term health.

![T1R Structure and Signaling](image)

**T1R Structure and Signaling**

The umami and sweet taste receptors are heteromeric, G-protein-coupled receptors (Fig. 1). T1R1-T1R3 is activated by glutamate and aspartate, as well as certain 5′-ribonucleotides, such as inosine and guanosine [1, 16]. T1R2-T1R3 is activated by a diverse set of stimuli including carbohydrates (mono- and disaccharides), sugar alcohols, sweet peptides and proteins, and other small molecule sweeteners [16]. In rodents, T1r3 ablation drastically reduces neural and behavior responses to umami and sweet stimuli [3]. Interestingly, sweet and umami taste are not entirely abolished in these animals, suggesting additional sensors for these stimuli. The residual responses to monosodium glutamate may be transduced by mGluRs [17, 18], and residual sweet responses may be transduced by components of the sodium potassium pump (Na+/K+-ATPase), sodium-glucose linked transporter 1 (SGLT1), and glucose transporters (GLUTs) in taste cells [19].

T1Rs are expressed on taste cells, which are arranged in groups called taste buds. Taste buds are distributed in distinct loci throughout the oral cavity, each of which is innervated by branches of the 7th, 9th, and 10th cranial nerves [20]. Taste buds are found on the fungiform papillae on the anterior tongue, the foliate and circumvallate papillae on the posterior tongue, and the smooth epithelia of the soft palate and the pharynx [20]. An often cited
but inaccurate belief is that specific regions of the oral cavity are solely responsible for specific taste modalities [21]. Although certain regions of the oral cavity are particularly responsive to certain taste qualities, all taste modalities can be elicited in all regions. Sweet and umami taste transduction begins when taste stimuli enter the taste bud pore and bind T1Rs on taste cells, which are electrically active, specialized, epithelial cells. Taste receptor binding can activate GTP-binding proteins, which begin the intracellular signaling cascade leading to taste cell depolarization and neurotransmitter (e.g., ATP, serotonin) release [22]. The signal is then carried to the brain by depolarized primary afferent taste neurons. The brain represents taste from unique patterns of activity across large networks of neurons, connecting opercular, insular, and orbito-frontal cortices, among other regions [20].

### T1Rs Guide Food Selection

Taste is a highly adaptive chemical sense. We use our sense of taste when foraging to identify the chemical makeup of a potential food source in order to assess its nutrient content. Appetitive taste stimuli reinforce the consumption of needed nutrients. Aversive stimuli, on the other hand, discourage the consumption of potential toxins or harmful microbes.

Umami taste guides the consumption of foods rich in free amino acids, which are essential for survival. Monosodium glutamate, a primary elicitor of umami taste, enhances the palatability of foods [23]. Umami taste is hypothesized to have evolved to guide the ingestion of foods rich in free amino acids, including certain vegetables and meats, as well as fermented, aged, or cooked foods [24]. Similarly, salty tastes identify sodium and other ions which serve a host of physiological functions, including the maintenance of membrane potentials and regulation of blood volume. Sweet taste identifies sugar-rich foods. The ability to identify sweet foodstuffs containing sugars may have been critical for the survival of human ancestors [25]. Given that all species of living apes other than humans are largely frugivorous, the diets of human ancestors were likely comprised predominantly of fruits. If so, sweet taste perception would be key for the identification of nourishing foods. Sour taste indicates the presence of acid, which is aversive at high levels and appetitive at low levels, especially when mixed with sugar (such as in fruit) [25]. Bitter taste, which is aversive at high intensities and can induce nausea, is adaptive because it deters us from consuming large quantities of toxins [26].

The critical link between taste perception and food ingestion is highlighted in patients with taste disorders. Taste sensitivity can be partially lost (hypogeusia) or entirely lost (ageusia) due to various causes at the cellular and organ level stemming from aging, disease states, and medical therapies [27]. Taste is also lost in patients receiving radiotherapy (head and neck areas). Loss of taste sensitivity is associated with unintentional weight loss and reduced quality of life [28, 29]. Taste and flavor enhancement have been successfully employed as a means of increasing food intake and improving health status in elderly patients [30].

Sweet taste is a particularly important topic with regards to human health. Our innate attraction to sweet-tasting foods, which served our ancestors in the tropical forests, has since become a public health concern. Carbohydrate-rich foods are no longer scarce, thanks to advances in agriculture and technology. The amount of food energy available per capita has increased to the point that the major nutritional challenge for humans of industrialized nations has shifted from undernutrition to overnutrition [31]. The prevalence of conditions related to overnutrition such as obesity, type 2 diabetes mellitus, and fatty liver disease increased dramatically in the latter half of the 20th century [32]. The epidemic of nutrition-related diseases has been attributed to a long list of factors, but one of the most often cited causes is the overconsumption of added-sugar foods, including sugar-sweetened beverages [33]. High-potency sweeteners (HPS), which bind and activate T1Rs to stimulate sweet taste, present a low- or no-calorie alternative to sugar consumption. Although some observational studies have shown that “diet” beverage consumption is not associated with weight loss [34, 35], several clinical studies have found that they can be effective tools for achieving weight loss [36, 37]. As will be discussed below, the recent discovery of taste receptors in metabolically active tissues has generated intense interest in the potential health impacts of HPS.
Taste Perception Primes Regulatory Physiology

Consuming a carbohydrate-rich meal causes a dramatic change in blood glucose [38]. It is important to defend against such changes because excessive amounts of glucose in the blood can damage blood vessels, glycosylate proteins, and promote the pathogenesis of chronic disease [39, 40]. As Ivan Pavlov demonstrated, associated food cues or the perception of food in the oral cavity can trigger digestive responses [41]. These responses are entirely independent of food ingestion, as evidenced by the fact that Pavlov observed them in fistulated animals and with very small stimulus volumes. They are absent, however, in vagotomized animals. Pavlov termed these phenomena “psychic reflexes” because they are neurally mediated. Currently, these effects are called cephalic phase responses. Cephalic phase insulin response (CPIR) exerts powerful effects on our bodies’ responses to food ingestion. CPIR is a small, transient increase in plasma insulin that occurs before exogenous glucose appears in the blood [42]. The effects of CPIR can be observed by infusing glucose intravenously with and without sham feeding. When glucose infusion is paired with sham feeding (which stimulates CPIR), the resulting plasma glucose AUC is approximately 30% lower than the glucose AUC without sham feeding [43, 44]. Considering that the magnitude of CPIR is relatively small, its effects on postprandial glucose are striking.

In humans and animals, saccharides elicit CPIR [45–47]. Although this might suggest that CPIR is mediated by T1Rs, the sensory mechanisms underlying CPIR are unclear. HPS do not reliably elicit cephalic phase responses, which suggests that CPIR may be mediated by T1R-independent carbohydrate detection in the oral cavity [48–50]. More recently, it was shown that oral stimulation with glucose stimulates CPIR in T1R knockout animals [46]. And fructose, which does not bind SGLT1, fails to stimulate CPIR. These findings support the hypothesis that SGLT1 may be responsible for non-T1R-mediated taste responses [19].

T1Rs May Facilitate Glucose Absorption

In addition to their roles in conscious taste perception, T1Rs may help guide post-oral absorption and metabolism of nutrients. Within the last decade, taste receptors have been identified in the intestine [5], stomach [11], liver [6], pancreas [6], adipocytes [7], skeletal muscle [8], heart [10], brain [9], testes [12], and bladder [13] (Fig. 2). Recent research has largely focused on the functions of T1Rs in the intestine and pancreas. In these tissues, it is thought that T1Rs serve as sensors that stimulate luminal glucose absorption as well as blood glucose clearance. Because blood glucose dysregulation is a hallmark of diabetes mellitus and its comorbidities, the role of T1Rs in glucose metabolism is a subject of growing interest.

In the intestine, T1Rs have been shown to activate processes involved in luminal glucose absorption, including glucose transporter expression and gut hormone secretion [5]. To briefly review the mechanisms of glucose absorption, glucose is taken up in the lumen by SGLT1. SGLT1 is an active transporter that uses the sodium gradient to move glucose across the apical membrane of the enterocyte. Glucose is transported out of the enterocyte and into the circulation through glucose transporter 2 (GLUT2) via facilitated diffusion. When luminal glucose concentration is high, GLUT2 translocates to the apical membrane to enhance glucose absorption [51]. SGLT1 expression also increases in response to carbohydrate feeding [52].

It is thought that T1Rs in the intestine act as sensors to detect glucose levels and coordinate absorptive responses. This hypothesis is based upon several lines of evidence from studies in animal models. T1R3 knockout mice show blunted SGLT1 expression and glucose absorption in response to sugar ingestion relative to wild-type mice.

Fig. 2. Type 1 taste receptors are expressed throughout the body.
T1Rs in Taste and Metabolism

[5]. And intestinal perfusion with HPS (which bind and activate T1R2-T1R3) upregulates apical translocation of GLUT2 and glucose absorption [14]. Further, the addition of HPS to a low-carbohydrate diet increases luminal SGLT1 expression, and this effect is dependent on T1R3 expression [5]. T1Rs are also implicated in the secretion of incretins in the gut, which potentiate glucose-stimulated insulin secretion. T1Rs are expressed on the surface of enteroendocrine L-cells, which secrete GLP-1 when exposed to HPS [53, 54]. This effect is blocked by lactisole, a T1R3 antagonist [54]. T1R3 ablation abolishes the GLP-1 response to glucose in the intestine [53].

Based upon these findings, it is hypothesized that T1R activation in L-cells stimulates the secretion of incretins, like GLP-1, which upregulate glucose transporter expression elsewhere in the lumen via paracrine signaling and ultimately increase glucose absorption [5]. This hypothesis is supported by a study in humans showing that elevated duodenal T1R2 expression is associated with increased glucose absorption [55]. However, several clinical studies have shown that HPS consumption (which theoretically stimulates luminal T1Rs) does not acutely enhance glucose absorption [56, 57]. Further clinical trials are needed to determine whether T1Rs influence glucose absorption in humans.

**T1Rs May Promote Plasma Glucose Clearance**

The finding that T1R activation in the intestine stimulates GLP-1 secretion is particularly striking because it implies a role for T1Rs in insulin secretion and blood glucose clearance. GLP-1 is an incretin hormone, which potentiates glucose-stimulated insulin secretion in the pancreas. The “incretin effect” describes the phenomenon whereby a fixed amount of glucose elicits a greater insulin response when administered orally relative to intravenous administration [58]. As a consequence of the enhanced insulin response, the incretin effect improves glucose clearance and results in lower postprandial glucose responses. The incretin effect is due primarily to GLP-1 and gastric inhibitory peptide (GIP) [59]. In addition to promoting acute insulin responses, the incretin hormones also promote beta cell proliferation [60]. The incretin effect is impaired in type 2 diabetes mellitus (T2DM) [61]. In T2DM, GIP sensitivity is impaired [62]. GLP-1 sensitivity remains intact, but its abundance is reduced [62]. Because GLP-1 remains effective in T2DM, it is a particularly attractive candidate for pharmaceutical therapies. GLP-1 receptor mimetic drugs such as liraglutide and exenatide are effective diabetes treatments [63]. The incretin hormones are degraded by dipeptidyl peptidase-IV (DPP-IV). Presently, DPP-IV inhibitors are also prescribed to control glycemia in diabetics [64].

The notion that T1Rs play a role in glucose clearance is further supported by studies showing that T1Rs are expressed in pancreatic beta cells in humans and mice [6, 65]. Murine beta cells secrete insulin when exposed to HPS, and this effect is blocked by sweet taste inhibitors [65, 66]. Furthermore, when glucose is administered via intraperitoneal injection (which bypasses oral and intestinal taste receptors), T1R3 knockout mice display drastically reduced insulin responses and heightened plasma glucose compared to wild types [15]. Thus, in these animals, pancreatic T1Rs influence insulin response and glucose tolerance independent of preabsorptive responses. The observation that T1R knockout animals are glucose intolerant underlines the potential importance of T1Rs in glucose clearance. In sum, it is hypothesized that T1Rs in the oral cavity inform food selection, intestinal T1Rs facilitate glucose absorption, and pancreatic T1Rs stimulate glucose clearance into cells (Fig. 3).

It remains unclear, however, whether T1Rs influence insulin secretion or glucose clearance in humans. Several clinical studies have examined whether HPS ingestion (which presumably activates extra-oral taste receptors) elicits changes in blood sugar and insulin. HPS consumption in the absence of glucose has been consistently shown to have no effect on GLP-1, insulin, and glucose [67–69]. However, when consumed prior to or in combination with a glucose load, HPS elicit striking, albeit mixed, effects in some studies. To date, only 9 studies have examined the effect of an HPS on measures of glucose tolerance [56, 57, 70–76] (Table 1). Only 1 study has shown a significant increase in plasma insulin responses, and interestingly there were no effects on GLP-1 or blood sugar outcomes [70]. In contrast, a later study showed that HPS enhanced GLP-1, reduced blood sugar, and had no effect on insulin responses [73]. Three studies have shown significant enhancement of GLP-1 responses with no effects on blood sugar or insulin [56, 71, 72]. Three studies showed no effects on any outcomes [57, 74–76]. These discrepancies remain to be explained but may be due to differences in patient populations, HPS products used, HPS doses, and method of delivery (pre-load vs. concomitant consumption with sugar). HPS vary widely in terms of chemical structure, potency, maximal activity, and metabolism. For instance, whereas aspartame does not enter the circulation because it is degraded to its amino acid constituents in the alimentary tract, acesulfame potassi-
um is absorbed in the intestine and excreted entirely in urine. It is also likely that oral ingestion of small doses of HPS may be an ineffective means of studying pancreatic T1R activation, given that most HPS are poorly absorbed and the pancreas is exposed to little dietary HPS.

**T1Rs in Modern Diets**

As described above, T1R knockout animals show drastic impairments in glucose tolerance and hormone secretion relative to wild types when fed standard chow diets [15]. In this context, the absence of T1R function represents a substantial metabolic disadvantage. The picture changes, however, when these animals are fed obesogenic diets. In a study of carbohydrate-induced obesity, wild-type mice became obese when their diets were supplemented with a 34% sucrose solution, but T1R3 knockouts did not [77]. The effect was independent of caloric intake, which suggests that the effect was due to differences in carbohydrate utilization between strains. However, when diets were supplemented with more palatable solutions containing lipid, both wild types and knockouts became obese. In a study of animals fed high-fat (Western) diets, T1R2 and T1R3 knockouts had smaller adipocytes and reduced adiposity relative to wild types [78]. In a similar study, T1R2 knockout animals had reduced fat mass, reduced liver triglyceride accumulation, and increased lean mass relative to wild types [79]. In addition, T1R2 knockouts were protected against diet-induced hyperinsulinemia. T1R2 knockouts were hyperphagic relative to controls and showed increased carbohydrate oxidation, which provides further evidence that the effects were driven by differences in carbohydrate utilization.

These studies show that in obesogenic environments, the absence of T1R function confers metabolic benefits. On the surface, this contradicts the notion that T1Rs were important to the survival of our species. There are clear differences, however, between the lifestyles of ancestral and modern humans. It was likely imperative for human ancestors to identify a potential food source before ingesting it, lest they face the consequences of starvation or toxin ingestion. It would have also been adaptive for early humans to efficiently absorb nutrients and store fat in the event that food availability became limited in the future. In modern times, however, nourishing food sources abound and humans face challenges stemming from overnutrition. A reduction in efficiency might now impart a benefit, as illustrated by the use of acarbose (a drug which inhibits carbohydrate digestion) to treat diabetes.

More work is needed to determine the mechanisms through which T1R ablation protects against diet-induced metabolic dysfunction. Because T1Rs are knocked out whole-body in these animals, it is unclear whether the observed effects are due to their activity in the gut, pancreas, adipose, or elsewhere. Reduced T1R activity in the pancreas may explain the observed protection against hyperinsulinemia, which in turn may reduce liver fat accumulation and adipocyte hypertrophy [79]. T1Rs are also
Table 1. Clinical trials examining the effects of HPS on OGTT outcomes yield inconsistent results

<table>
<thead>
<tr>
<th>First author [Ref.], year</th>
<th>Subjects</th>
<th>Design</th>
<th>Effects of HPS on GLP-1, insulin, and glucose</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown [71], 2009</td>
<td>Healthy (n = 22)</td>
<td>Subjects consumed 240 mL stimuli prior to OGTT; crossover design; stimuli: – cola sweetened with 68 mg sucrlose + 41 mg acesulfame potassium – carbonated water</td>
<td>Diet cola increased GLP-1 response to OGTT relative to water No effect on glucose or insulin</td>
</tr>
<tr>
<td>Brown [76], 2011</td>
<td>Healthy (n = 8)</td>
<td>Subjects consumed 355 mL stimuli; crossover design; stimuli: – water – water + 50 g sucrose – water + 6 g sucrlose – water + 50 g sucrlose + 6 g Splenda</td>
<td>No effect of HPS on glucose or insulin responses</td>
</tr>
<tr>
<td>Brown [72], 2012</td>
<td>Healthy (n = 25) T1DM (n = 9) T2DM (n = 10)</td>
<td>Subjects consumed 240 mL stimuli prior to OGTT; crossover design; stimuli: – diet soda containing 26 mg acesulfame potassium + 46 mg sucrlose – carbonated water</td>
<td>Diet soda increased GLP-1 response to OGTT relative to water (only in T1DM and healthy subjects) No effect on glucose</td>
</tr>
<tr>
<td>Pepino [70], 2013</td>
<td>Morbidly obese (n = 17)</td>
<td>Subjects consumed 60 mL stimuli prior to OGTT; crossover design; stimuli: – water + 48 mg sucrlose – water</td>
<td>Sucrelose increased glucose and insulin responses to OGTT No effect on GLP-1</td>
</tr>
<tr>
<td>Wu [75], 2013</td>
<td>Healthy (n = 10)</td>
<td>Subjects consumed 240 mL stimuli prior to OGTT; crossover design; stimuli: – water – water + 52 mg sucrlose – water + 200 mg acesulfame potassium – water + 46 mg sucrlose + 26 mg acesulfame potassium</td>
<td>No effect of HPS on glucose or insulin responses</td>
</tr>
<tr>
<td>Bryant [74], 2014</td>
<td>Healthy (n = 10)</td>
<td>Subjects consumed 250 mL stimuli; crossover design; stimuli: – water – water + 45 g glucose – water + 45 g glucose + 150 mg aspartame – water + 45 g glucose + 20 mg saccharin – water + 45 g glucose + 85 mg acesulfame potassium</td>
<td>No effect of HPS on glucose response</td>
</tr>
<tr>
<td>Temizkan [73], 2015</td>
<td>Healthy (n = 8) T2DM (n = 8)</td>
<td>Subjects consumed 200 mL stimuli prior to OGTT; crossover design; stimuli: – water – water + 72 mg aspartame – water + 24 mg sucrlose</td>
<td>Sucrelose increased GLP-1 and decreased glucose responses to OGTT No effect on insulin</td>
</tr>
<tr>
<td>Sylvetsky [56], 2016</td>
<td>Arm 1: healthy (n = 30) Arm 2: healthy (n = 31)</td>
<td>Conducted in 2 arms; subjects consumed 355 mL stimuli prior to OGTT; crossover design; stimuli: <em>Arm 1</em> – water – water + 68 mg sucrlose – water + 170 mg sucrlose – water + 250 mg sucrlose <em>Arm 2</em> – carbonated water – diet soda containing 68 mg sucrlose + 41 mg acesulfame potassium – diet soda containing 18 mg sucrlose + 18 mg acesulfame potassium + 57 mg aspartame – carbonated water + 68 mg sucrlose + 41 mg acesulfame potassium</td>
<td><em>Arm 1</em> No effect of HPS on GLP-1, glucose, or insulin <em>Arm 2</em> Diet soda containing 68 mg sucrlose + 41 mg acesulfame potassium increased GLP-1 response relative to water No effect on glucose or insulin</td>
</tr>
<tr>
<td>Karimian Azari [57], 2017</td>
<td>Healthy (n = 10)</td>
<td>Subjects consumed stimuli prior to OGTT; crossover design; stimuli: – water – water + 300 ppm saccharin – water + 500 ppm lactisole (T1R3 inverse agonist) – water + 300 ppm saccharin + 500 ppm lactisole</td>
<td>No effect of saccharin on GLP-1, glucose, or insulin Lactisole increased insulin response to OGTT</td>
</tr>
</tbody>
</table>

HPS, high-potency sweetener; OGTT, oral glucose tolerance test; T1DM, type 1 diabetes mellitus; T2DM, type 2 diabetes mellitus.
expressed in adipocytes [7], and it is possible that their ablation may alter lipid metabolism. The effects of T1R ablation on lipid metabolism are particularly intriguing because clofibric acid, a blood-lipid-lowering prescription drug, inhibits T1R3 in vitro and blocks sweet and umami taste in vivo [80–82]. Moreover, the physiological effects of T1R ablation appear to overlap with the physiological effects of clofibric acid treatment. Both reduce ectopic lipid accumulation [79, 83] and improve insulinemia [79, 84]. Clofibric acid is thought to exert its effects through PPAR α activation [85], but its effects on extra-oral T1Rs have not been examined in vivo. Further clinical studies with clofibric acid or other T1R inhibitors such as lactisole may be helpful in clarifying the contribution of T1Rs to metabolic outcomes.

Conclusion
T1Rs facilitate the identification and assimilation of nutrients. T1Rs are important receptors in the transduction of sweet and umami tastes, which help to ensure the consumption of sugars and amino acids. Recently, T1Rs have been identified in metabolically active tissues throughout the body. Preliminary work indicates that they promote absorptive and hormonal responses to food ingestion. T1Rs were highly adaptive for human ancestors who needed to quickly evaluate the nutritive value of foods and efficiently store fuel. However, in modern, obesogenic environments, overstimulation of these responses may not be beneficial to long-term health. To that point, studies in knockout animals suggest that T1R inactivation may protect against diet-induced conditions such as obesity, hyperinsulinemia, and liver steatosis. Further research is needed to clarify the functions of T1Rs in humans and to determine whether their activation or inhibition can be leveraged to influence metabolic outcomes.

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References


T1Rs in Taste and Metabolism

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The sensory and motor experiences associated with feeding, the type, variety, and timing of foods, their flavors, smells, and textures, as well as the social and emotional context of feeding, all contribute substantially to cognitive, social, and emotional maturation.

**Key insights**
A child’s first taste experiences are primarily sweet, starting before birth and continuing throughout breastfeeding. Sweetness is not just of nutritive significance, but also invokes powerful social and emotional connotations for the infant. During the introduction of complementary feeding, infants gain exposure to a wide variety of novel foods and flavors. Not only do infants learn eating skills, but this phase also sets the stage for the child’s later dietary habits. Parenting skills play a critical role in shaping the toddler’s emerging dietary pattern, laying the groundwork for future eating habits and nutrition.

**Current knowledge**
The American Academy of Pediatrics Committee on Nutrition recommends that infants be introduced to solid foods as a complement to breastfeeding at around 6 months of age, although the exact timing depends upon the infant and the family circumstances. The primal response to sweetness is initially an advantage, when the sweetness of breastmilk encourages consumption and soothes the neonate. Later, however, the inappropriate introduction of sweetened non-milk solids and beverages increases the newborn’s risk of later obesity and may discourage the acceptance of foods with bitter or sour tastes. Studies have shown that up to 60% of infants are introduced to foods and beverages containing added sugars, a major threat to diet quality.

**Practical implications**
The infant’s natural preference for sweet taste can be harnessed to reinforce the introduction and acceptance of healthy items such as whole fruits and vegetables. The strategy of pairing sweet foods with those which are sour or bitter can help in gaining acceptance. Between 6 and 12 months of age, parents should introduce as many flavors, colors, textures, and tastes from the main food groups, coupled with breast milk or formula. Repeated exposure is important to achieve acceptance of a new food item: some infants may need to be exposed 10–15 times to an item before they accept it. Pairing bitter or sour foods with a familiar and well-liked food or flavor, such as sweet, salty, or fat (termed “flavor-flavor learning”) may enhance acceptance.

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**Recommended reading**
Sweetness: Developmental and Functional Effects

Savoring Sweet: Sugars in Infant and Toddler Feeding

Robert D. Murray

The Ohio State University School of Medicine, Columbus, OH, USA

Key Messages

• Sweetness from natural and added sugars is integral to the infant and toddler feeding experience.
• The timing, amount, and nutritional quality of complementary foods and beverages introduced from 6 to 24 months fuels not only the child’s rapid physical growth but also the extensive expansion of the brain.
• Parenting skills are a critical factor in shaping the toddler’s first dietary pattern, which lays a foundation for food preferences, eating habits, and future nutrition.

Keywords

Complementary foods · Added sugars · Sweet · Infant · Toddler · Parenting · Dietary pattern

Abstract

During the first years of life, the sweetness of sugars has a capacity to hinder or to help in laying a strong nutritional foundation for food preferences that often extend over a lifetime. Aside from supplying 4 g/kcal of energy, sugars are non-nutritive. However, sugars have a powerful attribute, sweetness, which strongly influences human food preference. A child’s first relationship with sweet taste begins even before birth and continues to evolve throughout complementary feeding. The sweetness of breastmilk encourages consumption and soothes the neonate. Conversely, inappropriate introduction of non-milk solids and beverages that are sweet at 0–4 months of age raises the newborn’s risk for later obesity and may discourage the acceptance of other bitter or sour foods. Although cereals, fruits, 100% fruit juices, and some grains have naturally occurring sugars that impart sweet flavor notes, there is no clear role for added sugars between 6 and 12 months of age. Yet, 60% of infants are introduced to foods and beverages containing added sugars, threatening diet quality. Pairing foods with naturally occurring sugars, such as fruits, with foods that tend to be resisted initially, such as vegetables, can mask bitterness and promote acceptance. Utilizing the infants’ extraordinary capacity for sensory-motor exploration is another strategy to expose them repeatedly to challenging tastes and flavors. The transitional year, as breast milk and infant formula are withdrawn, is a time when nutritional needs are high and diet quality often precarious. Rapid growth, along with brain and cognitive development, demand high-quality nutrition. Snacks are necessary both for energy and valuable nutrients. However, the selection of snack foods often exposes toddlers to items that offer concentrated energy with low nutrient value. Recent trends suggest a rapid fall in added sugars among infants and toddlers. Parenting practices that use small amounts of sugars to promote nutrient-rich foods from all 5 food groups can enhance rather than hinder their child’s emerging dietary pattern.
A Singular Need for Diet Quality

The first 1,000 days of life represent a true singularity. Growth and organ development established during fetal life continue after birth. Linear growth increases by 7 inches (18 cm) in the first year, another 4–5 inches in the second year, and doubles birth length by 5 years. Weight doubles in just 4 months and triples by a year, then quintuples by 5 years [1, 2]. However, nutrients in the first months not only support increased bone, muscle, and tissue mass but also are substantially utilized for the continuing development of several highly metabolic organs, such as the gastrointestinal (GI) tract, the immune system, the central nervous system, the cardio-respiratory system, and the kidneys. As a result, a human’s maximal basal metabolic rate (BMR) occurs during the first few years.

More than just a food source, breast milk is a complex bioactive fluid with a broad array of components that aid immunity, promote digestion, regulate hormonal signaling, stimulate organ development, modulate inflammation, and ensure a stable transition to postnatal life [3, 4]. Breast milk stimulates rapid postnatal organ maturation, particularly of the GI tract and brain. Motility, which is rudimentary at birth, coordinates over months, paralleling changes in the gut nervous system. Similarly, gastric, intestinal, and pancreatic digestive functions develop gradually in response to daily exposure to nutrients [5]. In essence, the GI tract refines its absorptive, nervous, and immune functions through a process of sampling, analyzing, responding to, and signaling the body about the contents of swallowed material, including nutrients, allergens, microbes, and a variety of chemicals. An entire secondary digestive system is established through bacterial colonization, a process that leads to a stable, protective symbiosis by the age of 2 years [6, 7]. Colonization patterns differ between breastfed and formula-fed babies, vaginal and C-section babies, term and preterm babies. The choice of feeding affects the microflora, which in turn affects GI function, stimulates the gut immune system, and helps to set the body’s metabolism during this critical window of time [3].

Over half of the infant’s BMR is accounted for by brain development alone [2] (Fig. 1). At delivery, information from all 5 senses begins to trigger synaptogenesis, forming connections at a rate estimated to approach 700 per second [8]. Starting with a simple “birthday kit” of rudimentary reflexes, the infant will engage in intense daily sensory-motor exploration, resulting in increasingly complex skills that correlate with brain expansion. By 12 months, the infant brain will have doubled and by 36 months tripled in volume to nearly 85% of its ultimate adult size, based almost exclusively on synapse formation and myelination of axons [8]. The singular expansion of neuronal connections and brain volume in the first years presents a vital need for many different nutrients (Table 1).

During this critical period, feeding has consequences far beyond corporal growth. The sensory and motor experiences associated with feeding, the type, variety, and timing of foods, their flavors, smells, and textures, as well as the social and emotional context of feeding, all contribute substantially to cognitive, social, and emotional maturation [9]. All higher cognitive performance is based on this platform of sensory and motor development [8].
as linear growth, weight gain, and tissue enlargement depend on complete, quality nutrition, so too does the development and function of the brain. A child’s attention span, affect, learning capacity, memory, and motivation all are affected by diet quality [9–11].

**Sweetness Supports the Newborn**

Due to the combined nutritive and bioactive properties of breast milk, the American Academy of Pediatrics (AAP) strongly encourages its introduction for every baby, including premature infants, from the first feeding and throughout the first year [1]. It has long been known that breast milk’s hedonic properties encourage avid sucking and higher volume intake by the newborn [12–14]. Newborns have an innate preference for sweet flavor. Human milk also contains the odorants furaneol and maltol, both of which have a sweet caramelized smell [16]. In humans, evidence of a preference for sweetness has even been reported before birth. When the non-nutritive sweetener saccharin was injected into the amniotic fluid of the mother, the fetus swallowed more rapidly [16]. Likewise, newborns (term and preterm) given sucrose increased the frequency and strength of sucking, relative to water or an unflavored pacifier. Irrespective of calories, sweetness evokes a positive hedonic response across the lifespan. Infants and children consistently prefer more concentrated sucrose than adults do. This affective response may result from energy needs related to their rapid growth and high BMR. Infant preferences can be assessed by 2 complementary research methods: observation and coding of facial responses and consumption of solutions that vary in taste and concentration [17, 18].

**Table 1. Nutrient roles in brain growth, development, and function**

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Functions and Effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitamin B₁ (thiamine)</td>
<td>rapidly depleted; glucose utilization; modulation of cognition; language development; neurotransmitter synthesis and mood</td>
</tr>
<tr>
<td>Vitamins B₁, B₆, B₁₂, and choline, tryptophan, tyrosine, histidine, threonine, copper</td>
<td>synthesis of neurotransmitters</td>
</tr>
<tr>
<td>Vitamin B₁₂</td>
<td>cognition, language, myelination</td>
</tr>
<tr>
<td>Vitamin C</td>
<td>antioxidant protection; cognition; hippocampal development and spatial memory; myelin production</td>
</tr>
<tr>
<td>Vitamin D</td>
<td>prevention of neuronal damage; dopamine development</td>
</tr>
<tr>
<td>Vitamin E</td>
<td>antioxidant protection; cell membrane integrity; omega-3 fatty acid (DHA) protection;</td>
</tr>
<tr>
<td>Flavonoids/phytonutrients</td>
<td>protect neuronal integrity and enhance function; anti-inflammatory; promote memory, learning, cognition; neurogenesis</td>
</tr>
<tr>
<td>Iron</td>
<td>oxygen delivery; synthesis and integrity of myelin; neurotransmitter synthesis; information processing; hippocampal structure and memory</td>
</tr>
<tr>
<td>Magnesium</td>
<td>energy; ion regulation; neural plasticity; neuroprotection</td>
</tr>
<tr>
<td>Zinc</td>
<td>axonal and synaptic transmission; enzymatic control of cell proliferation and neurogenesis; taste perception; neuromotor function</td>
</tr>
<tr>
<td>Iodine</td>
<td>(via thyroid) cellular energy metabolism</td>
</tr>
<tr>
<td>Omega-3 PUFA</td>
<td>cognition, visual development</td>
</tr>
<tr>
<td>Lutein</td>
<td>macular protection; concentrates in infant hippocampus and visual, auditory, and frontal cortex; optical density correlates with processing speed, language, memory</td>
</tr>
</tbody>
</table>
sweetness from the first day of life. The nursing newborn quickly associates the satiating sweetness of milk with the nurturing closeness of maternal contact, linking sensations of warmth, touch, taste, and smell. The newborn brain shows widespread cortical activation during the act of breastfeeding, including hypothalamic, limbic, and brain stem areas [19, 20]. Brain responses during feeding reflect the pleasurable tastes and smells, the satiation of hunger, as well as the calming, and even analgesic, effects of consuming milk.

Breast milk also provides infants with their first experiences with the complex flavors of food by passing sensory elements from the maternal diet directly to the baby. Studies suggest that these ever-changing flavor notes prime the newborn for later acceptance of novel foods and beverages when they are introduced [21]. Taste, touch, and smell during feeding are integrated by the newborn’s brain to form perceptions that we characterize as flavor [22]. In this way, feeding serves as an integral part of the daily sensory-motor exploration that typifies infants’ first year of life and contributes directly to their brain development. Infant formulas have been designed to mirror the macro- and micronutrients of breast milk and more recently have incorporated its first bioactive ingredient, human milk oligosaccharides. Lactose in infant formula offers the bottle-fed infant the same sweetness as breast milk, but formula cannot deliver the complex, ever-changing flavors, smells, and mouth feel experienced by the breast fed infant.

Feeding serves as an integral part of the daily sensory-motor exploration that typifies infants’ first year of life and contributes directly to their brain development

Inappropriate Early Introduction of Complementary Foods

Parental and caregiver feeding trends for infants and toddlers are tracked through the National Health and Examination Survey (NHANES), a nationally representative, cross-sectional survey on the nutrition and health status of the US population conducted by the National Center for Health Statistics, in which participants complete in-home interviews, physical examinations, dietary interviews, and post-examination components [23]. Additional data are available through the Nestlé Feeding Infants and Toddler Study (FITS), a recurring cross-sectional survey of feeding among a representative sample of US children from birth to 4 years, overseen by researchers within the Gerber Medical Division [24, 25].

The AAP recommends exclusive breastfeeding for the first 6 months as ideal. No other solids or liquids except breastmilk or commercial infant formula should be offered until the infant is at least 4–6 months of age, with the exception of fluoride and iron supplementation for specific populations [1]. A recent review of NHANES data was conducted examining infant feeding over 2 different time periods (2005–2008 and 2009–2012) [26]. Breast and infant formula feeding rates remained stable, with formula being more commonly consumed. Early introduction of non-milk items declined significantly from 50.4 to 39.6% of infants during this span, largely due to falling consumption of infant cereals and fruit juices in the first 5 months of life. The most commonly offered items were sweet tasting: infant cereals (25.9%), fruits (13.6%), and 100% fruit juice. Of note, consumption of the latter fell sharply from almost 13 to 6.5% of infants between the two survey periods. Offerings of snacks, desserts, and sweetened beverages did not change over time, with inappropriate exposure still seen in 5% of infants [26]. The reasons for caregivers offering non-milk foods in the first 6 months are varied, but one important factor may be confusion over conflicting messages about whether foods should initially be offered after 4 months, “around 6 months,” or after 6 months of age [1, 27, 28].

The Introduction to Complementary Feeding: 6–12 Months

Complementary feeding (CF), the provision of first non-milk foods and beverages, is necessary not merely to boost energy and nutrients at a critical period of growth, but equally to ensure acceptance of a wide variety of novel foods and flavors [17, 29, 30]. With time, CF also should introduce increasingly complex food textures, developing the infant’s nascent chewing and swallowing skills [31]. Encouraging food acceptance entails not only food selection, but also positive parenting behaviors that promote their consumption [17, 30]. This phase of feeding sets the stage for the toddler’s first appreciable dietary pattern, the components of which generally remain relatively stable after 24 months of age.

The AAP Committee on Nutrition recommends that infants be introduced to solid foods as a complement to milk-based feeding “around 6 months of age” [1]. This is not based solely on chronologic age. The infant’s devel-
Consumption of sugar-sweetened beverages (other than those that were rejected initially. Bitter or sour foods may be more readily tried if offered first when hunger is highest.

The strategy of pairing sweet flavored foods with foods on the bitter end of the spectrum also can be helpful [17, 25]. The duality between preference for sweet and aversion to bitter and sour is a crucial factor for successful CF. As innately preferred tastes, saltiness and sweetness can be used to mask or minimize less pleasant, largely bitter tastes in novel foods. When paired together, using a strategy termed “associative” or “flavor-flavor” learning, tastes and flavors with high likability can be utilized to encourage acceptance of foods commonly rejected [16, 17]. However, fruits with naturally occurring sugars can be used to the same advantage during this period as foods with added sugars, leading many experts to question whether added sugars have any role in CF during the 6- to 12-month period [33, 45].

The young child uses seeing, touching, smelling, tasting, and eventually swallowing of novel foods as the path to gradual acceptance [17, 29]. The standard practice of introducing at least 2% to the diets of 6- to 12-month-old infants, were cow milk, fruits, and mixed grain-based dishes. Inappropriate introduction of cow milk prior to 12 months was noted in 14%, but this has been declining with time [26, 34, 35]. Fruits, baby beverages, and 100% juice combined to contribute roughly 3–4% to total carbohydrates, with sweet grain desserts contributing another 1.8% [34]. 100% fruit juice contributed only 1.5% of daily energy, but comprised over one-half of all the fruit servings consumed.

Concerns about the frequency of low-nutrient foods offered to infants, as well as the over-representation of a few individual food items, such as sugars, starches, and juices, has led to close scrutiny of CF [30, 36–38]. The contribution of 100% juice to total energy is small among 6- to 12-month-olds and generally is consumed within the guidelines of the AAP, providing a valuable source of nutrients [39]. However, in a recent revision of the 2005 AAP policy statement on 100% juice consumption, the Committee on Nutrition urged that 100% juice be excluded from the 6- to 12-month CF recommendations [40]. The committee was concerned about reinforcing intensely sweet preferences early in the exploratory phase of eating. The Committee on Nutrition also theorized that minimizing sweet liquids might lessen future consumption of sweet beverages, lowering the risk for obesity. A recent meta-analysis by Auerbach et al. [41] found almost no support for a connection between 100% juice and obesity, however.

The infant’s preference for sweet is easily reinforced during the 6- to 12-month stage of complementary food exploration, often to the detriment of diet quality [17, 42]. Consumption of sugar-sweetened beverages (other than breast milk, infant formula, or 100% fruit juice) was noted in 25% of 6- to 12-month-olds and in 50% of 12- to 24-month-olds [26, 35]. Acceptable toddler daily limits for added sugars have not been set, but for children over the age of 2 years and for adults, both the DGA and the WHO have recommended a limit for added sugars of <10% of total energy [43, 44]. Promoting food acceptance in the 6- to 12-month period entails a conscious effort to introduce the baby to as many different flavors, colors, textures, and taste combinations as possible from each of the 5 food groups: fruits, vegetables, (whole) grains, dairy, and protein sources. If caregivers regularly offer a rotating variety of food experiences throughout the day of nutrient-rich foods in appropriate serving sizes, coupled with 32 ounces per day of breast milk or iron-containing infant formula, there will be little room for added sugars [26, 45].

Research suggests that repeated exposure is central to infant acceptance of novel CF. Young children learn to prefer familiar foods [17, 30]. Neophobia – the resistance to trying new tastes or textures – is a reflection of infant temperament and of the intensity of the infant’s perception of a bitter sensation. Other factors include the feeding environment, parental expectations, distractions, lack of feeding routines, and family eating habits [29]. The number of exposures needed to induce acceptance of novel flavors and textures may exceed 10 or even 15 times [17, 30, 42]. It is incumbent on caregivers to persist in offering new foods repeatedly and in novel ways, especially those that were rejected initially. Bitter or sour foods may be more readily tried if offered first when hunger is highest.

The young child uses seeing, touching, smelling, tasting, and eventually swallowing of novel foods as the path to gradual acceptance [17, 29]. The standard practice of
exposing the infant to new flavors, smells, tastes, and textures through spoon-feeding by an adult may not be the only or the best strategy. A baby-led approach to feeding has been advocated in which advances in CF are determined and directed by the baby, relying on the child’s curiosity [46–49]. This type of self-feeding mirrors the strategy used by Clara Davis in her landmark studies on toddler self-feeding in the 1920s [50]. Although the research is still in an early stage, baby-led weaning may have much to offer as a strategy to encourage acceptance of novel foods through exploration and repeated exposure.

**Transitional Year CF: 12–24 Months**

The transition period is arguably the most important year in human nutrition for a variety of reasons: (1) high energy and nutrient needs to support rapid linear and organic growth, coupled with continued organic development, (2) extensive expansion and wiring of brain due to sensory and motor exploration, including that during feeding, (3) formative first experiences with a variety of foods, (4) establishment of food and flavor preferences, as well as eating habits, and (5) development of social, emotional, and cognitive skills. All require sound nutrition.

In the transition year, sweetness and sugars show both positive and negative effects on the toddler diet. Breast milk and/or formula are usually replaced by cow milk in the second year [38]. Less reliance on milks requires a greater emphasis on consuming CF. Baby foods are replaced by finger foods, table foods, and eventually family foods. Snacks assume an influential role in the diet. The toddler’s acceptance of new CF becomes a crucial factor in diet quality. Because this transition can be challenging for many toddlers, some researchers have suggested extending breastfeeding, formula feeding, or the use of “growing-up milks” well into the second year [51, 52], although the majority of toddlers have energy and nutrient intakes that appear to match recommendations [35, 53–55].

The dietary pattern of the toddler and its future effect on development, health, and academic outcomes is a burgeoning area of research [11, 38, 56–58]. The DGA 2015 [43] described the concept of a dietary pattern by stating that, “over the course of any given day, week, or year, individuals consume foods and beverages in combination – an eating pattern. An eating pattern is more than the sum of its parts; it represents the totality of what individuals habitually eat and drink, and these dietary components act synergistically in relation to health.” Within the toddler dietary pattern, added sugars and sweet flavors can have a positive impact if limited in quantity and associated with nutrient-rich foods. Yet, current surveys raise several concerns about the timing, amount, and overall contribution of sugars to the toddler dietary pattern [26, 34, 35, 37, 38].

Moshfegh and colleagues [35, 54] described current dietary intakes among toddlers between 1 and 2 years of age based on the “What We Eat in America” component of the 2011–2012 NHANES. Energy averaged 1,335 kcal/day over this period, with daily energy increasing from 1,201 to 1,441 kcal between 12 and 24 months, respectively. Carbohydrates comprised 55% of daily energy, with total sugars making up one-half of those calories. Natural sugars comprised 40% of total energy, mostly from dairy sources, while added sugars contributed an average of 10%. Moshfegh et al. [35] noted that 40% of the toddlers were consuming more than the 10% average.

Miles and Siega-Riz [26] examined trends in toddler feeding between 2005 and 2012 using the NHANES data. The more recent survey showed a further fall in vegetable intake in the transition year, along with no discernable improvement in whole fruit. On the other hand, the survey found a marked decline in infant cookies and biscuits at 6–12 months that carried over into the 12- to 24-month period, with cookies and sweets falling steeply. However, the authors cited wide differences among non-Hispanic white, non-Hispanic blacks, and Mexican-Americans in terms of food and beverage trends during the CF period. The decline in sugar consumption among infants and toddlers mirrors that of the US population generally, with a steadily falling consumption since 2000, despite a continued rise in obesity rates (Fig. 2) [26, 59, 60].

Combining NHANES 2009–2010 data with the Food Patterns Equivalent Database, Welsh and Figueroa [36] looked specifically at total and added sugars in the diets of toddlers aged 1–2 years. In their analysis, nearly all toddlers (99%) were found to consume some added sugars daily, accounting for 8.4% of their total daily energy. Between 6 and 24 months, added sugar intake rose linearly. Previous research indicates that added sugars will continue to climb in the preschool- and school-age years, accounting for nearly 17% of daily energy in adolescence.
Fig. 2. Since 2000, as obesity rates have continued to rise, consumption of sugars has fallen sharply among the US population, including infants and toddlers, with sweetened drinks and candies leading the fall. Reprinted with permission from Guyenet [60].

US sugar intake vs. obesity prevalence, 1980–2013

Since 2000, as obesity rates have continued to rise, consumption of sugars has fallen sharply among the US population, including infants and toddlers, with sweetened drinks and candies leading the fall. Reprinted with permission from Guyenet [60].

High-energy, low-quality foods were commonly offered to toddlers between 6 and 24 months. For instance, 1 in 3 toddlers consumed candy, 2 in 5 consumed dessert items, such as cakes, cookies, and pastries, while 1 in 10 consumed frozen dairy desserts [35]. Nutrient-rich items, such as yogurt, sweetened fruits, and sweetened cereals also contributed added sugars, but added substantially to the nutrient pool as well [36]. Grimes et al. [34] pointed out several sources of added sugars or naturally sweet-tasting foods and beverages that provide a wide array of nutrients to the toddler dietary pattern, including milks, yogurts, cereals, grain-based products, 100% fruit juices, baby foods, fruits, and starchy vegetables.

Beverages accounted for 25% of a toddler’s daily energy. Milk, the most common beverage, contributed the most nutrients and the most energy among the category [26, 35, 36]. Milk, mainly whole milk, was consumed by 80% of toddlers at least once daily, averaging 1½ cups per day, close to recommendations. Milk was followed by water and 100% fruit juice [35, 36]. Other beverages with added sugars included sweetened fruit drinks (24%), soft drinks (6–14%), and flavored milks (7–9%). Sweetened juices and drinks were the leading source of added sugars. Of the 26 g/day average intake of added sugars, 10.5 g were attributed to beverages [36]. However, a recent NHANES analysis from 2013–2014, showed a sharp fall-off in the consumption of 100% fruit juice (-16%), fruit drinks (-9%), and soft drinks (-13%) over the prior decade [35]. Added sugars from beverages contributed only 2.7% to the total daily energy of 12- to 24-month-old children. Still, studies show that after the transition year, sweetened beverage consumption rises steadily throughout childhood and adolescence [36].

Almost 100% of US children and adolescents snack at least once daily [61]. Snacks are necessary for young children in order to augment daily energy and provide crucial micronutrients [62]. Yet, many caregivers described snacks as an emotional indulgence, independent of the child’s primary diet [63]. The most recent NHANES data show that daily snacking frequency among toddlers has increased from 69 to 98% prevalence over the past 3 decades. There has been a corresponding rise in the contribution of snacks to total daily energy, from 16% in 1977 to 31% in 2014, accounting for more daily calories than are consumed at breakfast, lunch, or dinner meals [35]. FITS 2008 data on a low-income population showed that nearly half were given 3–4 snacks per day [59]. On the other hand, the nutrient profile derived from toddler snacking is generally good [34, 35, 59]. NHANES data showed that snacking not only contributed 20% of protein, 35% of carbohydrate, 42% of total fat, and 32% of saturated fat, but also 25% of daily fiber, 35% of calcium, over 20% of iron, 31% of potassium, and approximately 35% of vitamins C, D, and E [35].

The white potato accounted for one-third of all vegetables among infants and one-half among toddlers [26]. Although yellow vegetables were consumed by nearly 50% during the 6- to 12-month period, mostly from baby food, fewer than 20% consumed them in the second year. Green vegetables were consumed by only 7.5% of toddlers, despite decades of public health admonitions. Pairing bitter or sour foods with a familiar and well-liked food or flavor, such as sweet, salty, or fat, (so-called “flavor-learning”) has been suggested to enhance acceptance [17]. Some but not all studies have shown that small amounts of sugar or salt help overcome a young child’s resistance. A recent AAP policy statement suggested that small amounts of fats, sodium, and added sugars should be utilized specifically to promote increased consumption of nutrient-rich foods in all 5 food groups [64].

An ideal upper limit for the contribution of total and added sugars to total daily energy has not been established for toddlers. For children above the age of 2 years, as well as adolescents and adults, the DGA 2015 and the WHO both have recommended that added sugars be limited to less than 10 percent [43, 44]. This limit was not established using toxicity data, but rather was based on modeling of food patterns with varying intakes of added sugars. To meet food group and nutrient needs within appropriate calorie limits, added sugars needed to contrib-
ute less than 10% of energy. Similar modeling of CF within the toddler dietary pattern has not been done. Still, the same rationale applies. Thoughtful use of added sugars tied with high-nutrient foods and beverages may aid consumption of nutrient-laden foods among toddlers in this crucial phase of life.

Sweetness is a central component of the feeding experiences of the fetus, infant, and toddler. Both natural and added sugars comprise a substantial part of daily carbohydrate intake. Research suggests that early food preferences track over the lifespan. This has raised concerns that early eating habits may fuel obesity. However, obesity is a complex, multifactorial disorder and not solely the result of diet. Although many caregivers use added sugars at inappropriate times, in excessive portions, and too commonly, it is not the whole story. Added sugars may be a valuable tool to help the young child assimilate less readily accepted foods, enhance diet quality, and lay a strong foundation for life-long nutrition.

**Disclosure Statement**

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