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Early Influences on the Development of Food Preferences

Review

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The ability to perceive flavors begins *in utero* with the development and early functioning of the gustatory and olfactory systems. Because both amniotic fluid and breast milk contain molecules derived from the mother's diet, learning about flavors in foods begins in the womb and during early infancy. This early experience serves as the foundation for the continuing development of food preferences across the lifespan, and is shaped by the interplay of biological, social, and environmental factors. Shortly after birth, young infants show characteristic taste preferences: sweet and umami elicit positive responses; bitter and sour elicit negative responses. These taste preferences may reflect a biological drive towards foods that are calorie- and protein-dense and an aversion to foods that are poisonous or toxic. Early likes and dislikes are influenced by these innate preferences, but are also modifiable. Repeated exposure to novel or disliked foods that occurs in a positive, supportive environment may promote the acceptance of and eventually a preference for those foods. Alternatively, children who are pressured to eat certain foods may show decreased preference for those foods later on. With increasing age, the influence of a number of factors, such as peers and food availability, continue to mold food preferences and eating behaviors.

Introduction

The development of food preferences begins at conception and continues across the life course. This development involves a complex interplay of biological tendencies and environmental influences. Available data suggest that infants are born 'hard-wired' to prefer tastes that signal beneficial nutrients (for example, sweet tastes signal calories) and to reject tastes that signal harmful compounds (for example, bitter tastes signal poison) [1]. Infants and young children show considerable plasticity in preferences [2], however, enabling them to accept and learn to prefer the foods that are available within their particular cultural and culinary milieu [3].

The aim of this review is to compile research from several disciplines to provide a comprehensive overview of the factors that contribute to the development of food preferences during the prenatal, neonatal, infancy and early childhood periods. We start with an overview of the development of the senses taste and smell, and then consider the biological and social influences on food preferences across early development. We will focus on the development of food preferences in children who are typically developing, as research on children with developmental delays is beyond the scope of our review. We focus on early life, not to discount the ability of food preferences to develop during later childhood, adolescence and adulthood, but rather because early life has been highlighted as a sensitive period for the development of sensory perception and food preferences [4–6]. As will be further discussed below, strong correlations have been found between food preferences during early childhood and preferences in later childhood [7], adolescence [8] and young adulthood [9], implicating early experience as a foundation for food preference development across the life course.

Development of Gustatory and Olfactory Systems

Taste and flavor perception are central to the development of food preferences, as both taste and flavor preferences have been highlighted as primary drivers of food preferences during early life [10]. Additionally, food preferences are the strongest predictors of young children's food acceptance [11,12]. Thus, an understanding of how and when gustatory and olfactory systems develop is an important basis for examining the development of food preferences and acceptance.

Taste sensations result from activation of the gustatory system and are limited to the sensations of sweet, bitter, sour, salty, and umami or savory; however, evidence is mounting for additional basic tastes, such as fat and calcium [13,14]. In contrast, thousands of different odors stimulate the olfactory system to create smell sensations. Flavor perception results from the integration of taste and smell sensory systems: the combination of odors sensed orthonasally and retro-nasally with tastes sensed by receptors in the oral cavity (Figure 1) is what creates flavor sensations, such as vanilla or strawberry.

The capacity for sensing postnatal flavors begins *in utero* with the development of the gustatory and olfactory systems. These systems are functionally mature and have achieved adult-like form by the end of gestation. The presence of gustatory and olfactory systems *in utero* provides the opportunity for early sensory learning that is theorized to prepare the fetus for postnatal experiences.

Both the morphological and functional development of taste cells begin in the first trimester. Fungiform, foliate, and circumvallate papillae appear by the 10th week of gestation [15–17], and taste cell synaptogenesis is increasingly apparent during weeks 8–13 [18]. Taste papillae are functionally mature by the beginning of the second trimester [18,19], and the number and distribution of papillae that are present during late gestation are strikingly similar to those seen in childhood and adulthood [20].

Development of the olfactory system also begins during the first trimester. By the 8th week of gestation, the olfactory bulb has differentiated from the forebrain, and primary olfactory receptors have appeared [21]. Olfactory marker proteins, an indication of olfactory receptor maturity, are present by the 28th–29th week of gestation [22]. The nasal plugs blocking the nasal passages dissolve between the 16th and 36th week of gestation, allowing the nasal passages to be bathed in amniotic fluid [23].

Development of the gustatory and olfactory systems continues postnatally, but data on this development in humans are limited due to a lack of longitudinal studies examining

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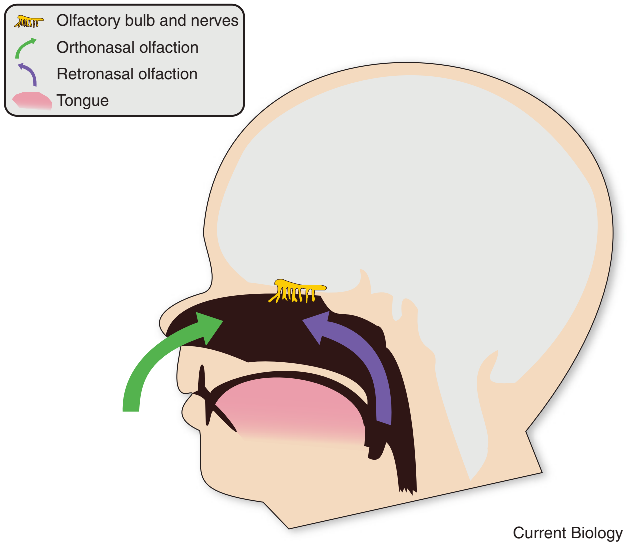

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Figure 1. The anatomy of flavor perception.

Sagittal section of an infant head illustrating orthonasal (green arrow) and retronasal (purple arrow) routes of olfaction and the spatial relation between the oral cavity and olfactory bulb. (Adapted with permission from [161].)

intra-individual changes in these systems [10,24]. Available research examining age differences in gustatory and olfactory anatomy suggests the morphological development of these systems is fairly complete at birth [25,26], but age-related increases have been noted for brain activation and higher-order information processing in response to gustatory and olfactory cues (see [24] for a review). Thus, postnatal changes in these systems appear to be focused on maturity of neural systems underlying sensory perception [10,27].

Biological Influences on Food Preferences

Genetic Influences on Taste Perception and Preferences

Food preferences appear to be partially genetically determined, with high coefficients of heritability for preferences for protein foods, fruit, vegetables and desserts [28,29]. One mechanism underlying genetic influences on food preferences may be variation in taste perception and preferences. Recent research has identified several genes related to individual differences in sweet [30], umami [31–33], and bitter [34,35] taste perception. The perception of these tastes involves G-coupled protein receptors encoded by the *TAS1R* and *TAS2R* taste receptor gene families (in contrast, salty and sour tastes are transduced by ion channels in taste receptor cells [36,37]). Single nucleotide polymorphisms in these gene families are associated with functional variance in sweet, umami and bitter perception, but the mechanisms underlying the majority of these associations have yet to be elucidated [38].

Variance in bitter taste perception has been the most extensively studied and much of this research has focused on the *TAS2R38* gene. Two common alleles at the *TAS2R38* locus are associated with variation in sensitivity to two synthetic substances, phenylthiocarbamide (PTC) and 6-n-propylthiouracil (PROP) [34,35,39]. In particular, an individual's *TAS2R38* genotype predicts whether these two substances taste strongly bitter, moderately bitter, or are tasteless. Adults with the bitter-sensitive alleles of *TAS2R38* also rate foods such as brassica vegetables (watercress, mustard greens, turnip, broccoli [40]) as more bitter compared to adults with the bitter-insensitive alleles. This sensitivity may translate to preferences, as some studies indicate both adults [41,42] and young children [43,44] with greater sensitivity to the bitter taste of PTC and PROP report lower preferences for and consumption of bitter foods (such as bitter vegetables, grapefruit juice, green tea, soy products). However, data for an association between bitter sensitivity and preferences remain equivocal, as other studies have found no association between PTC or PROP sensitivity and food preferences and intake [45–47].

Genetic sensitivity to bitter taste may also influence sensitivity to and preferences for other tastes. For example, individuals more sensitive to the bitterness of PROP have heightened perception of sweet tastes from sucrose [48] and saccharin [49,50]. Mennella and colleagues [51] reported that children with the bitter-sensitive *TAS2R38* genotype had higher preferences for sweet foods and beverages. However, race/ethnicity was more strongly associated with sweet preferences than *TAS2R38* genotype in adults, suggesting culture and experience may come to override effects of genotype on food preferences during later life [51].

Unlearned Behavioral Responses to Taste Stimuli

Preferences for taste stimuli appear to be strongly influenced by innate factors [52] and are believed to be present *in utero*. Direct study of fetal origins of unlearned responses to taste stimuli is difficult given obvious ethical and practical limitations of experimentation with human fetuses. However, previous researchers have used indirect strategies, such as measurement of fetal response to chemical input and study of premature infants as a proxy for fetal development, to understand affective responses to taste stimuli *in utero*.

The fetus both inhales and swallows significant amounts of amniotic fluid by late gestation [23,53]. The amniotic fluid contains many constituents, ranging from nutrients (such as glucose and amino acids [54]) to the tastants and flavors of the mother's dietary and environmental exposures [3]. DeSnoo [55] found that injection of a sweet-tasting stimulus into the amniotic fluid stimulated fetal swallowing, while Liley [54] found that injection of a bitter stimulus inhibited fetal swallowing. These reactions have been interpreted to be positive and negative hedonic responses to sweet and bitter tasting stimuli [56,57], respectively. Provision of glucose or sucrose solutions to premature infants (born 25–36 weeks gestational age) elicited stronger and more frequent sucking compared to provision of water, responses the authors interpreted to be indicative of positive affect or acceptance [58,59]. In contrast, pure lemon juice stimulates salivation, vigorous sucking, or retching, whereas quinine (a bitter stimulus) retards sucking. This body of indirect evidence suggests that the fetus shows specific responses to taste stimuli in the amniotic fluid during late gestation.

Newborn infants' responses to tastants are similar to those seen *in utero*. Figure 2 provides examples of characteristic responses of neonates to sweet and bitter tastes [60]. Neonates given sweet or umami solutions exhibit behaviors that are interpreted to be positive hedonic responses [61]: elevation of the corners of the mouth, lip and finger sucking, lip smacking, and rhythmic tongue protrusions [62–64]. Neonates also exhibit increased rates of sucking and ingest larger volumes in response to sweet and umami solutions compared to bitter, sour, salty and neutral

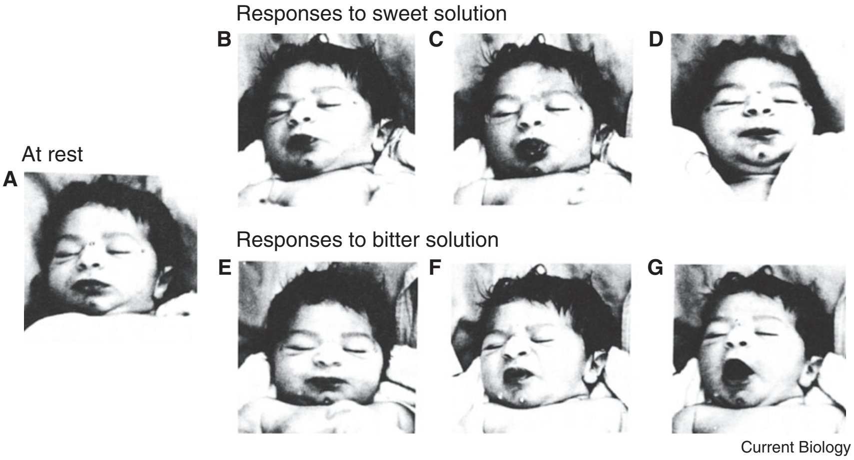

Figure 2. Characteristic responses of neonates to sweet and bitter tastes.

These photographs illustrate the range of neonate's characteristic responses to sweet (sucrose) and bitter (quinine) solutions. The top row of photographs (B–D) contains responses to the sweet solution and the bottom row of photographs (E–G) contains responses to the bitter solution. (A) The resting face is characterized by relaxed, closed eyes and neutral expression, and can serve as a comparison for examining responses to sweet and bitter tastes. (B) Some infants show a subtle response to sweet taste. (C) The response to sweet is often characterized by sucking. (D) Elevation of the corners of the mouth or pulling in of the lower lip is also a common reaction to sweet taste. (E) Some infants show a subtle response to bitter taste. (F) The response to bitter is often characterized by head turning and grimacing. (G) Gaping is also a common reaction to bitter taste. (Adapted with permission from [60].)

stimuli [65–68]. Neonates given bitter solutions exhibit behaviors that are interpreted to be negative hedonic responses [60,63]: frowning, arm flailing, head shaking, gaping, and nose wrinkling [62,69], as well as a disruption in sucking behavior [69,70]. Evidence for neonates' responses to sour tastes is equivocal, as some neonates exhibit lip pursing, gaping, nose wrinkling, arm flailing and dampened sucking behavior [69,70], while others show positive hedonic behaviors such as lip smacking and rhythmic tongue protrusions [62,71]. Salt taste is unique in that neonates exhibit neutral facial responses to salty solutions [27,72], but also show lower rates of sucking compared to when given water [68,73]. However, a preference for salt taste develops after 4 months of age and continues into childhood [27].

Unlearned taste preferences seen during the fetal and neonatal periods are maintained and heightened during later infancy and childhood and then diminish during adolescence and adulthood. Compared to adults, children are more sensitive to bitter tastes [51,74,75]. Children also prefer solutions with significantly greater concentrations of sweet [51,76–78], salt [79], and sour [80,81] tastes compared to adults. These trends are likely a result of both biology and, as will be discussed in the following sections, experiential learning.

Specific affective reactions to differing taste and smell stimuli are believed to be predominantly unlearned and reflex-like for several reasons: first, they are remarkably similar across species [62,82] and cultures [71,72]; second, they occur in infants with anencephaly [83,84]; and third, they can be reliably elicited in a concentration-dependent manner in newborns with minimal extra-uterine taste and feeding experience [85]. These reactions may represent an evolutionary adaptive response to varied and uncertain food environments [86]. Young children are trying to learn what and how to eat; thus, it would be protective for children to be highly sensitive to the vast array of flavors and foods to which they are introduced.

Before food processing and labeling, human survival depended on correctly discriminating foods that were energy-dense and nutrient-rich from those that were toxic or rancid. In nature, sweetness is often associated with calorie-rich carbohydrate sources such as breast milk or fruit [87]; umami is associated with amino-acid or protein-rich foods, such as meats [88]; and salt signals the presence of an essential mineral [89]. In contrast, bitterness signals toxins or poisons [90] and sour signals the presence of strong acids [88]. Additionally, children may be most sensitive to certain tastes (for example, sweet) during periods of maximal growth [91,92], which has been hypothesized to help these children select foods that will best support rapid development [91]. Taken together, these data support the hypothesized evolutionary need for unlearned taste preferences and may partially explain changes in these preferences across the life course.

Food Neophobia

Over the course of the first few years of life, young children undergo a transition from a predominantly milk-based diet to one consisting of adult table foods [93]. Young children (especially 2–5 year olds) exhibit heightened levels of food neophobia during this time of rapid dietary change. Food neophobia is defined as an unwillingness to eat novel foods and is thought to be an adaptive behavior, ensuring children consume foods that are familiar and safe during a developmental period when children are being exposed to a vast number of new foods [94]. Rozin and colleagues [95,96] have shown that distaste — dislike of the sensory characteristics of a food — appears to be the strongest driver of neophobia in young children, followed by potential harm or sickness. Indeed, the two strongest predictors of young children's food preferences are familiarity and sweetness [97], reflecting the unlearned preferences that have been reviewed in this section. However, as will be discussed in the following sections, these innate tendencies are paired with a predisposition to learn from early experiences through associative learning [98,99] and repeated exposure [3,100,101], allowing the child to learn to accept and prefer the foods that are available within his particular environment.

Social Influences on Food Preferences

Early Sensitive Periods for Flavor Learning

Much is learned about the foods of the world long before they are ever directly consumed. Both amniotic fluid and breast milk contain tastants and odor volatiles from the mother's dietary and environmental exposures (for example, garlic [102], carrot [3], alcohol [103]). Experimental research suggests that these flavors, when presented repeatedly within the amniotic fluid and breast milk, influence the infants' feeding behaviors and preferences immediately after birth [104,105] and during weaning [3]. For example, infants whose mothers were randomized to consume carrot juice during the third trimester or during the first two months of lactation consumed greater amounts of, and showed fewer negative facial responses in response to, a carrot-flavored cereal compared to infants whose mothers did not drink carrot juice or eat carrots during pregnancy and lactation [3]. Thus, flavors within both the amniotic fluid and breast milk may help to guide infants toward flavors that will soon be experienced in foods by shaping early preferences.

The early flavor experience of formula-fed infants is markedly different from that of breast-fed infants. Psychophysical studies of human milk show that its predominant taste quality is sweetness, and it also provides a myriad of sensory experiences that are dynamic and vary both within and between mothers [106,107]. In contrast, the flavor experience of formula-fed infants is constant and unchanging, as the majority of formula-feeding mothers feed their infants a single type of formula [108]. Despite this constancy, each brand and type of formula has a unique flavor profile [109], ranging from low levels of sweet and sour tastes in cows' milk-based formulas (CMF), to sweet, sour, and bitter tastes in soy protein-based formulas (SPF) to savory, sour, and bitter tastes and unpleasant (to older children and adults) odor volatiles in extensive protein hydrolysate formulas (ePHF) [110]. These differences are attributed to differences in composition and processing [111].

Formula-fed infants also show preferences for the flavors experienced during early formula-feeding. Mennella and colleagues [112] showed that infants fed ePHF consumed greater amounts of savory, sour, and bitter-flavored cereal and made fewer facial expressions of distaste when fed bitter and savory cereals compared to breast- or CMF-fed infants. In contrast, CMF-fed infants showed preferences for sweet, salty, and sour cereals [112]. Other research suggests these preferences extend beyond weaning, as ePHF-fed infants showed greater preference for savory broths during later infancy [4] and greater preference for sour-flavored juices at ages 4–5 years compared to CMF-fed infants [113].

In sum, early flavor experiences, whether from amniotic fluid, breast milk, or formula, may shape early preferences. Furthermore, the influence of these preferences appears to extend into early childhood and translate to later food preferences. For these reasons, the prenatal and early postnatal periods have been described as sensitive periods for early flavor and food preference learning [4]. However, as will be discussed in the following section, social influences become increasingly important for the development of food preferences and may either support or counter the preferences learned during the prenatal and early postnatal periods.

Repeated Exposure, Associative Conditioning, and Parent Feeding Practices

Experimental studies illustrate that neophobic tendencies can be reduced and preferences can be increased by exposing infants and young children repeatedly to novel foods [100,101,114,115]. These studies suggest that young children need to be exposed to a novel food between 6 and 15 times before increases in intake and preferences are seen [100,101,114,115]. Furthermore, exposure needs to include tasting the food, as merely seeing [101] or learning [115] about a novel food on repeated occasions did not promote children's preferences for that food. A recent intervention study found that repeatedly exposing children to a novel food within a positive social environment was especially effective in increasing children's willingness to try and preference for the novel food, as well as other novel foods not targeted by the intervention [116]. These findings suggest the importance of both the act of repeatedly exposing children to new foods and the context within which this exposure occurs.

Post-ingestive consequences also influence preferences [98] and can facilitate the acceptance of previously disliked tastes, such as sour and bitter [117] (see [118] for a more in-depth discussion of the role of associative conditioning in shaping preferences). For example, children prefer flavors that are paired with energy-dense (as opposed to energy-dilute) foods [119]. When children have repeated opportunities to consume two different versions of the same food that differ in energy density (for example, a high-fat or low-fat pudding) and have distinct flavor cues, children show preference for the flavor paired with the higher energy-density version [98,99,120]. Research using animal models report similar findings [121,122], which suggests the predisposition to prefer foods that confer positive post-ingestive effects, as do energy-dense foods, is unlearned.

Parents may try to mold their children's food preferences by offering contingencies (for example, "if you eat your peas you can have ice cream for dessert", or "you cannot leave the table until you clean your plate") or pressuring children to eat (for example, "finish your soup"). These practices may have the immediate effect of increasing children's intake of the target food [123], but have the longer-term effect of decreasing children's preferences for the target food [124–127]. In essence, these practices devalue the target food relative to a contingency food and send the unintentional message to children that the target food is not preferable in and of itself.

Parents may also restrict children's access to palatable foods that are high in sugar, salt, and fat in an effort to decrease their children's preference for and intake of those foods [128–131]. However, when children were presented with two snack foods in a laboratory-based setting, one restricted and the other freely accessible, children showed a clear preference for the restricted food despite reporting no difference in preferences for the two foods prior to the restricted versus free-access presentations [132]. In addition, when later given free access to both snack foods, children exhibited a greater behavioral response and higher intake of the previously restricted snack food compared to the freely accessed snack food [132]. That these laboratory-based findings translate to free-living situations is supported by observational studies showing that parents who report higher levels of restriction have children who show higher preference for and intake of energy-dense snack foods when they are made freely available [128,130,133].

Cross-sectional and observational studies have shown that the foods that parents consume and make available to their children predict the types of foods their children consume [134–136]. Experimental studies have provided evidence that both adult and peer models are effective in promoting children's acceptance of and preferences for novel foods [137,138]. Thus, social facilitation, or an increase in a behavior in the presence of others displaying the same behavior [139], impacts children's intake patterns and likely serves to ensure that children are consuming foods that have been demonstrated by others to be safe. As children mature and become increasingly independent of their parents for food choices and acquisition, social modeling and food availability within the greater food environment (for example, food marketing, schools, community organizations) become increasingly influential on food preferences (a recent review by Fiese and Jones [140] provides an excellent overview of these broader influences).

Emerging Research on Neural Responses to Taste Stimuli

Emerging research has begun to focus on how neural responses to taste stimuli, a function of both unlearned and learned factors [24], may influence taste and food preferences. Much of this work has focused on neural responses to sweet taste (see [141] for a review). Stimulation of sweet receptors activates pleasure-generating reward centers in the brain [142] through circuitry and mechanisms very similar to or overlapping with that seen for the rewarding properties of alcohol and drugs [143] (indeed, it has been suggested that these addictive substances may be co-opting neural pathways originally designed for sweet tastes [144]). Thus, neural pathways linking sweet tastes to rewards may be partially responsible for innate preferences for sweet tastes, and may also be further strengthened by repeated exposure to and intake of sweet foods.

The hedonic value of sweet taste may be further accentuated by an analgesic effect of sweet taste during early childhood [145], which is also mediated by neural mechanisms [146]. Specifically, infants given sucrose or other sweet-tasting solutions after a painful stimuli, such as a heel stick, cried for a significantly shorter amount of time compared to when given water [145]. This effect is attributed to taste perception, not post-ingestive events, as intra-gastric administration of sucrose in preterm infants does not induce the same calming effects [147] and non-caloric sweeteners, such as aspartame, mimic the calming effects of sucrose [61]. This response is similar across infants of differing genders, gestational ages and postnatal ages at the time of testing [148,149], and continues into childhood [77,150,151]. Evidence for analgesic effects of sweet taste during adulthood are inconsistent [146,150].

Changes in Food Preferences after Childhood

Although much of food-preference development occurs during early childhood, food preferences continue to change during adolescence and adulthood [9,152]. The factors that influence this change become more complex as the individual matures (Figure 3) [153]. Adult food preferences are associated with age, sex, health status, education, and income [154,155], and the healthfulness of food preferences increases with increasing age [156,157]. *This indicates* a shift from primarily hedonic-based preferences early in life to preferences that involve consideration of the health, social, and economic impacts of foods later in life [158]. Additionally, advanced age brings additional considerations for flavor and food preferences, as older adults often experience declines in normal taste (hypogeusia) or smell (hyposmia) sensitivity, or distortion of normal taste (dysgeusia) or smell (dysomia) functioning, all of which can be attributed to normal aging (for example, reduction in number of taste buds) or certain disease states (such as Alzheimer's disease, medications, or surgical interventions) [159,160].

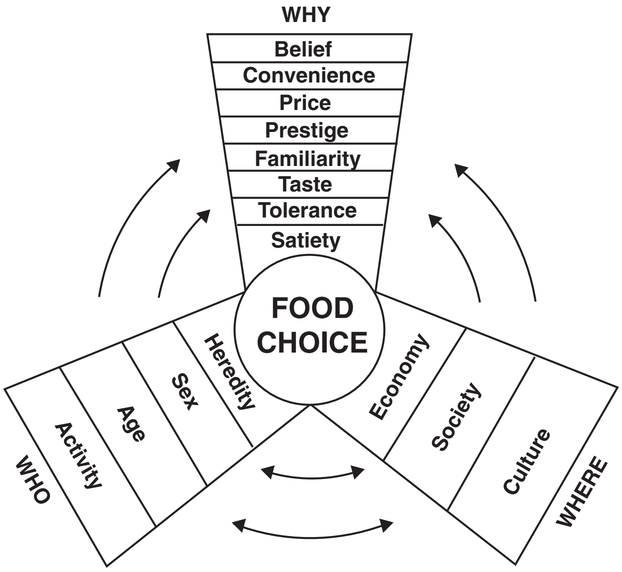

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Figure 3. Krondl's food perception model.

This model illustrates that food preferences and choices arise from a combination of three arms of influence: "Why?" or the sensory experiences and beliefs associated with a food; "Who?" or the biological needs of the individual; and "Where?" or the physical and social environment within which the food is acquired. (Adapted with kind permission of Springer Science+Business Media from [153].)

Conclusions

Each individual's unique preferences and aversions are based on predisposed biological tendencies, but are further cultivated and modified through experiential learning. Available data suggests that young children are biologically primed to prefer and consume foods that are sweet, salty, and savory, as well as flavors paired with energy density. Fortunately, preferences are malleable and are shaped in response to a number of social and environmental factors. Preferences are a strong driver of dietary intake in both children and adults [97,157]; thus, an understanding of these factors is an essential basis for understanding how preferences can be modified to best promote healthful diets across the life course.

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