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The flavor of life: perinatal development of odor and taste preferences[1]

Summary

Despite the importance of chemosensation in the regulation of ingestive behavior, we still know surprisingly little about the development of the olfactory, trigeminal and gustatory systems. All three, however, are functional to some degree prenatally, and by birth infants are able to respond to a wide range of odors and can clearly distinguish between the tastes of sweet, sour and bitter. Based on findings from our work in the rabbit, we report that learning of odors associated with the mother's diet can occur very early in development, even prenatally, that it can have a long-term influence on later food choice, and may even lead to enhanced, stimulus-specific sensitivity of the basic sensory apparatus. Whether comparable phenomena exist in human infants is not known, although our recent findings that nationalities differ in judgements of the pleasantness of food odors depending on whether these are recognized as representing familiar, culture-typical foods, suggests that it might. A cross-cultural study is currently in progress examining the influence of culture-specific childhood eating experiences on adult preferences for food-associated odors.

Keywords: innate preferences; odor learning; prenatal perception; cross-cultural differences; food-associated odors

Zusammenfassung

Obwohl die chemosensorischen Eigenschaften bei der Regulierung des Essverhaltens wichtig sind, wissen wir erstaunlich wenig über die Entwicklung des Riech- und Geschmacksystems und der diesbezüglichen Genussfunktion. Alle drei sind zu einem bestimmten Grad bereits intrauterin wirksam. Bei Geburt sind Neugeborene fähig, auf eine weite Spanne von Gerüchen zu reagieren und können eindeutig zwischen dem Geschmack süss, sauer und bitter unterscheiden. Aufgrund von Arbeiten mit Kaninchen wissen wir, dass das Lernen von Gerüchen über die Ernährung der Mutter sehr früh in der Entwicklung einsetzt, sogar schon pränatal, und dass dies einen langfristigen Effekt auf die spätere Nahrungswahl haben kann. Dies kann auch zu erhöhter reizspezifischer Sensitivität des Geruchapparats führen. Ob ähnliche Phänomene auch bei Menschen bestehen, ist noch zu wenig bekannt, muss aber vermutet werden. Denn verschiedene Nationalitäten unterscheiden sich in der Beurteilung von angenehmen Nahrungsgerüchen je nachdem, ob sie als familiäre und kulturtypische Nahrung erkannt werden. Zurzeit ist eine kulturübergreifende Studie im Gang, die den Einfluss des kulturspezifischen Ernährungsverhaltens von Kindern auf die späteren Präferenzen von nahrungsassoziierten Gerüchen im Erwachsenenalter untersucht.

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Introduction

Without doubt, the most important function of the chemical senses in humans is the role they play in the regulation of ingestive behavior – not only what we ingest, but at what age, at what time of day and how much. This is the case despite our otherwise strong dependence on visual information. No matter how appetizing the lobster might look on its carefully arranged bed of salad, if it smells "off", we will waste no time sending it back to the kitchen. Or to take a more positive example – the sudden smell of freshly baked bread on the way home on a cold winter's night. Who has not experienced the feeling of pleasure and sudden appetite generated by such food-associated aromas? It is surely surprising that despite the universal nature of such sensations we still know relatively little about their origin; when during development they emerge, to what extent they are shaped by experience, and their role in the long-term development of dietary preferences.

In seeking answers to these questions we are immediately confronted by one of the central issues in developmental biology and one of the traditionally hottest areas of debate in the behavioral sciences, the so-called nature-nurture issue. Briefly, this concerns the question to what extent characteristics – here preferences for particular odors and tastes – are innate, prewired and the result of genetic programming, and to what extent they are shaped by experience. Although the question of inborn versus learned is now considered a rather artificial dichotomy, with the two sets of factors usually resisting clear separation, it continues to provide a useful conceptual basis for analysis and discussion.

In this report we briefly consider evidence for the existence of innate, genetically determined chemosensory responses, followed by evidence for the role of early experience in shaping these. In particular, we will emphasise the role of experience, giving examples from our own work on responses to food-related odors in young rabbits and of human subjects from different cultural backgrounds. We argue that while there is good reason to believe that responses to chemosensory stimuli, particularly tastants, have been shaped by evolution and thus have a genetic basis, learning plays an important role in tuning the organism, human or infra human, to its particular chemosensory environment. Moreover, we report evidence that odor learning can occur very early in development, even prenatally, that it can be long-lasting, and may even lead to enhanced, stimulus-specific sensitivity of the basic sensory apparatus.

First, however, it is useful to consider briefly the developmental time course of human chemosensory systems, as well as the kinds of stimuli normally available for them to detect.

Development of chemosensation

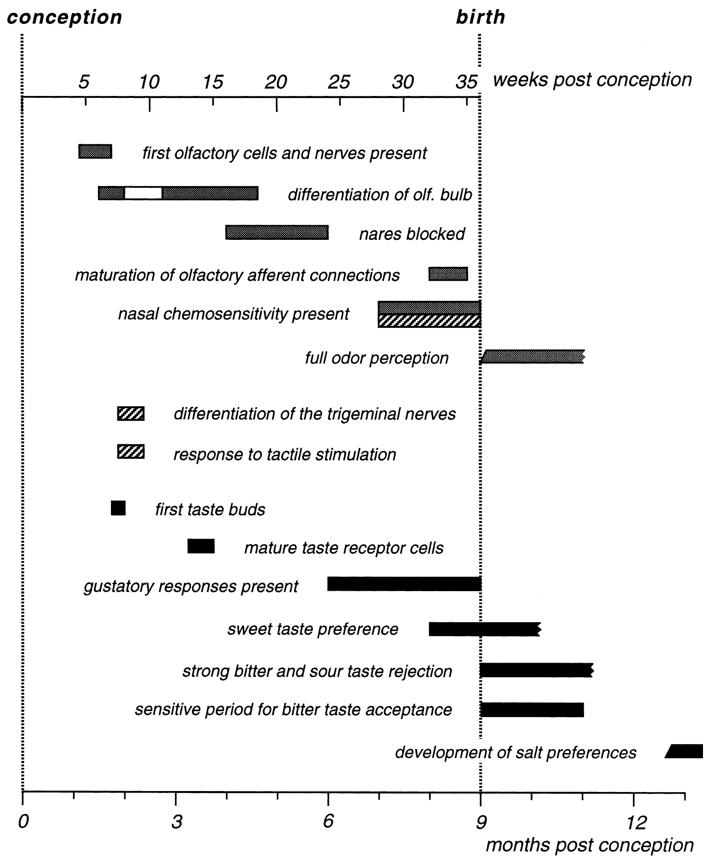
Providing a developmental account of chemosensation is a complex matter since it usually involves at least three distinct sensory systems: olfaction, taste and trigeminally-mediated sensation. In the context of ingestion, these operate simultaneously to produce what, in adults at least, is usually perceived as one integrated and unified sensation, flavor. The olfactory sensory receptors are located in the upper nasal cavity, taste receptors are located on the tongue, in the bucal cavity and at the back of the throat, while the chemosensitive free nerve endings of the trigeminus innervate, among other surfaces, the nasal and bucal mucosae. Chemical stimuli can reach the olfactory receptors not only via the usual orthonasal route but also from the mouth via the retronasal pharyngeal opening. This helps explain the important contribution of the sense of smell to flavor, and thus in judging the palatability and acceptability of foods [1].

All three systems are apparently functional during prenatal life (fig. 1). Anatomical reports and behavioral studies of preterm infants suggest that gustatory responses are already present by about prenatal week 24, and nasal chemosensitivity to odorants having both trigeminal and olfactory properties, by about prenatal week 28 [2–4]. Such evidence of early function is consistent with the recent report that newborn infants prefer the odor of their own amniotic fluid compared to that from a strange mother [5]. It is also supported by findings from a range of other mammalian species demonstrating that odors associated with the mother's diet can be learned prenatally and can influence the behavior of the young, including their food preferences, well into postnatal life [6–8]. More will be said about this below.

Whatever the situation in the human fetus, the few studies available suggest that infants are capable of perceiving a wide range of odors at

Figure 1

Perinatal development of the olfactory, trigeminal and gustatory systems (based on [2–4]).



birth [9]. In the case of tastes, however, the situation appears more complex. Whereas neonates are clearly able to perceive the sensations of sweet, sour and bitter, responding with facial expressions of acceptance to the first and with rejection to the other two [10, 11], responses to salty stimuli seem to develop somewhat later. Thus, whereas newborn infants show no particular behavioral response to salty solutions, at about four months they preferentially ingest weak saline solutions compared to plain water [12]. Furthermore, whereas newborns fail to show clear behavioral responses to some bitter substances such as low concentrations of urea, within two weeks they show clear rejection [13].

A notable characteristic of the chemosensory environment is its variety and complexity, even prenatally [2, 14]. In utero, the fetus is in continual contact with a wide range of molecules present in the amniotic fluid or the maternal circulation. These originate from substances ingested or produced by the mother, and later, produced by the fetus itself. Since even in the adult the olfactory epithelium is normally covered by a layer of mucous through which odor molecules must pass to reach the receptors, a liquid environment is not an impediment to olfaction. Furthermore, it is well established that at least some odorants can be perceived when present in the blood, probably by stimulating the olfactory receptors after diffusing out of the fine nasal capillaries [15].

The postnatal chemosensory environment is no less complex, with stimuli emanating from the mother, particularly from her skin and in the milk, probably among the most important in the immediate postnatal period. Certainly, infants are able to rapidly learn such stimuli and demonstrate a preference for familiar odors and tastes associated with their own mother within the first few postnatal days [2, 4, 16–18]. With the transition to solid food, the range of behaviorally relevant chemosensory information then expands rapidly [3].

Innate preferences

There are good adaptive reasons why humans could be expected to have evolved innate preferences for, or aversions to, particular chemical stimuli; the generally preferred taste of sweetness usually signals a substance of high caloric value, whereas the generally aversive taste of bitter often signals toxicity, for example, associated with the secondary chemical compounds produced by many plants as a defence against herbivores [19].

Evidence for the presence of innate responses is stronger for taste than for olfaction. This probably relates to the greater predictability of information coded by the basic taste sensations of sweet, sour, bitter and salty compared to the highly complex and essentially unpredictable olfactory world. Evidence for innate responses to tastants is provided by the facial expressions shown by newborns in response to gustatory stimuli reported above. Such responses are even seen in anencephalic infants, demonstrating that the neural mechanisms supporting these hedonic responses are located in the brain stem [20]. Innate, maturational changes in the taste system are also indicated by the fact that the developmental changes in the response to salty stimuli reported above emerge independently of experience or nutritional state [12].

Acquired preferences

We humans are omnivores par excellence, and the ability to colonize most of the planet has depended to a large degree on our capacity to take advantage of a wide range of nutritional niches. Omnivores, however, face two major challenges: the recognition and localization of optimal foods, and avoidance of toxic substances or foods of low nutritional value [21]. In the case of generalist feeders, it is simply not possible for the diversity of information relating to potential foods and non-foods to be encoded genetically, and the advantages of maintaining an open, flexible, yet sufficiently safe system have to be achieved by learning. In the case of ingestive behavior, the most essential of chemosensory-guided functions, we might suppose such learning to occur early in development.

Perinatal odor learning in the rabbit

For some time we have been investigating early odor learning in an animal model, the newborn rabbit. Rabbits show an unusual pattern of maternal care; they spend very little time with their young and only visit them once a day for nursing. The altricial young are born with eyes and ears closed and with poor motor coordination. The sense of smell, however, is well developed, and is of major importance in enabling the pups to locate the nipples and suckle. Interestingly, the mother produces a specific chemical signal, the so-called nipple-search pheromone, which reliably releases stereotyped search behavior and nipple attachment [22].

The pups are also able to associate other odors on their mother with nipple-search behavior and suckling, for example, artificial substances painted on her fur [23, 24]. This is reminiscent of findings that human infants also readily learn both natural and artificial odors associated with their mother [2, 25]. In the rabbit, this early learning is very rapid (one nursing episode) and achieved most effectively during the first few days, suggesting that it is characterised by a sensitive period and may represent a form of olfactory imprinting [26, 27].

A second type of learning occurs to ambient odors of the environment, for example, present in the nest [28]. Newborn rabbits simply exposed to artificial odorants for about a day demonstrate a preference to these when allowed to choose between them and another odor. This type of learning is not dependent on any obvious reward and probably serves to familiarize the young with their immediate odor environment.

Rabbit pups also learn odors originating from their mother's diet. We supplemented the lab chow diet of lactating does with either juniper berries or thyme, both plants which form part of the diet of rabbits in the wild. At weaning on day 28, pups were caged individually and presented with a "cafeteria" of lab chow, juniper berries or thyme. The first food chosen and amount of each eaten during the first week post-weaning demonstrated pups' food choice to be influenced by the diet of the mother. Pups raised by juniper-fed does ate significantly more juniper than pups from thyme-fed or control does, whereas pups from thyme-fed does ate significantly more thyme than the other two groups [29]. This learning is very robust and pups raised from weaning without further experience of the mother's diet still demonstrate a preference for it when tested as adults six months later [30].

Furthermore, pups exposed only in utero to juniper, and immediately after birth cross-fostered to control does, show as strong a preference for juniper as the pups described above receiving postnatal experience [8]. Pups

are able to express this learning soon after birth and when tested for odor preference in an arena on day 1, choose the side scented with the odor of their mother's diet [31]. This is consistent with findings in rats and sheep that odors associated with the mother's diet can also be learned in utero [6, 14, 16].
The significance of such early odor experience is reinforced by the finding that odor exposure in utero results in a stimulus-specific enhancement in sensitivity at the level of the olfactory epithelium. Electrical recordings were made from isolated olfactory epithelia of prenatally juniper-exposed and control pups during the application of juniper odor or a novel control odor, isoamyl acetate. The response to juniper odor relative to isoamyl acetate was significantly greater in juniper-exposed pups than in controls [31].
From a biological point of view it would seem to make sense for young mammals to be particularly receptive to stimuli associated with their mother. Mothers are individuals who have succeeded in surviving to reproductive age and, having had time to learn features of their environment such as the most nutritious and least poisonous plants, represent a source of information which can be relied upon and taken advantage of in making the risky transition to solid food.

Cross-cultural differences in the response to food-associated odors in humans

Although not directly related to the perinatal period, we have recently obtained evidence for marked, experience-dependent differences in the judgement of food odors from an inter-cultural study of adults.
To investigate the influence of experience on odor perception the responses of 40 Japanese and 44 age-matched German women to everyday, food-related odorants were compared. Subjects were presented with 6 "Japanese", 6 "European" and 6 "international" odorants and asked to rate them for intensity, familiarity, pleasantness and edibility, to describe associations elicited by them, and if possible, to name them. Significant differences were found between the two populations on all measures, with the close association between pleasantness ratings and edibility suggesting the particular influence of culture-specific eating habits on odor perception. Positive correlations between familiarity and pleasantness of the stimuli, strength of hedonic judgement and perceived intensity, and between familiarity and perceived intensity were also found in both groups and for most individuals. The generality of these findings was supported by very similar results obtained from testing 39 Mexican women with the same odorants [32, 33].
In summary, odors recognized as representing a familiar food will not only generally be judged as more pleasant, but also will be perceived to smell more intense than if they are not recognized as representing a familiar food. How early such differences in preferences for the odors of familiar, culturally-specific foods develop is not known. However, in a study of immigrant populations in Germany, Mexico and the United States this is currently under investigation.

Future perspectives

In conclusion, although chemosensation emerges early in life and newborn infants are capable of rapid olfactory and gustatory learning, we still know surprisingly little about this field of sensory development. For the pediatrician, two kinds of information should be particularly valuable:

- First, more detailed knowledge of early chemosensory experience. This would include more detailed information about the ages at which particular sensory capacities emerge, as well as the kinds of chemosensory experiences available to and made use of by infants. Among other clinical applications, such information could help to provide a more optimal sensory environment for premature infants.
- Second, information regarding the long-term effects of early chemosensory experience on ingestive behavior. Given the obvious practical difficulties of conducting controlled, longitudinal studies, we still have very little information about this in humans. However, given the growing evidence from animal studies for the role of early experience in shaping later chemosensory preferences, and first indications of sensitive periods for food-associated chemosensory learning in infants [4, 34], this subject certainly deserves more attention. Again, to

mention one area of possible clinical relevance, the evidence for durable prenatal learning of odorants associated with the mother's diet raises the question to what extent fetuses exposed even to low levels of agents such as alcohol may more readily develop a preference for such substances in later life. This is a significant biomedical issue in a broader sense and one which brings us back to the complexities of the nature-nurture debate mentioned in the introduction. Evidence for robust prenatal learning further blurs the distinction between inborn and learned responses, calling into question claims that behavioral problems such as alcoholism or over-consumption of fatty foods are genetically determined [35–37], and suggesting that early experience might play at least a facilitating role in the later expression of such behavioral tendencies.

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