

Developmental Changes of the Taste Sensation Depending on the Maturation of the Taste Bud and its Distribution in Mammals

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Behavioral experiments elucidated that newborn mammals must be able to distinguish differences of taste between preferable and aversive sapid solutions in order to continue their development (Steiner, 1973; Ganchrow *et al.*, 1986). Such a gustatory function must depend on the development of taste buds both before and after birth. The appearance and maturation of taste buds are different among the various subpopulations [fungiform (FF), foliate (FL), circumvallate (CV) papillae and soft palate (SP)] in the rat (Mistretta, 1972; Steiner, 1973; Ganchrow *et al.*, 1986; Hosley and Oakley, 1987; Harada *et al.*, 2000), hamster (Belecky and Smith, 1990) and marmoset (Yamaguchi *et al.*, 2001).

Among the total number of taste buds located within these different loci, at birth, the number of SP and FF taste buds with and without pores were more than a hundred, and the developmental curves for the SP and FF taste buds during the life span were similar (Harada *et al.*, 2000). The number increased and reached a steady level around 200 at 1 week of age. In contrast, the CV and FL contained only a few taste buds at birth, and the number continuously increased and reached around 400 at 4 weeks.

Since the existence of a taste pore must represent functional maturation, percentages of taste buds possessing a taste pore was calculated as a function of the postnatal age (Harada *et al.*, 2000). At birth, 53% of SP taste buds were observed, although FF contains only 12% of taste buds with a taste pore. At 1 week of age, 90% of SP taste buds contained a taste pore, indicating that maturation was almost complete. A similar maturation of FF taste buds occurred one or two weeks later in the SP. On the other hand, the maturation of taste buds within the CV and FF were delayed by a few weeks compared to those of the SP and FF. The distribution of taste buds on the SP was similar between those at birth, those at 8 weeks and even those at 24 months of age, indicating that the fundamental distribution pattern of taste buds on the SP was established at birth in the rat.

Similarly in the newborn marmoset, only 20% of 334 FF taste buds at day 1 possessed a taste pore (Yamaguchi *et al.*, 2001). Although the number of taste buds within the SP at day 1 was 182, and half of that for the FF, 39% of SP taste buds possessed taste pores which was twice that of FF taste buds. The SP taste buds were densely gathered together into several groups, and the fundamental patterns of their distribution were established at birth which was similar to what occurs in the rat.

These histological results from the rat and marmoset indicate that the maturation of taste buds within the SP precedes those within the other three types of papillae, suggesting that the functional maturation of SP taste buds also likely precedes those in other areas of the oral cavity.

Functional characteristics of the SP taste buds were also examined by recording responses from the greater superficial petrosal nerve (GSP) in the rat, and comparing these responses with those obtained from the chorda tympani (CT) (Harada *et al.*, 1994, 1997; Yamaguchi *et al.*, 2001). Responses from the GSP and CT nerves to six 0.5 M sugars showed that all six of the sugars, especially sucrose

produced robust responses in the GSP compared to the CT. Characteristics of greater responses to sweet substances in the GSP than in the CT was similar to those in the hamster (Harada and Smith, 1992). This specific responsiveness to sweet substances in the GSP suggest an important role of the GSP in mediating sweet information to the brain stem in these animals.

Results from a comparison of the responses to L- and D-amino acids in the CT and GSP in the rat revealed that the responses to HCl salts of D-basic amino acids were not significantly different compared to those to their enantiomer (Harada *et al.*, 1994). However, in the GSP, D-His-HCl produced a significantly larger response than L-His-HCl. As for the neutral amino acids, most of the L-neutral amino acids produced larger response in the CT than those to D-neutral amino acids. In contrast to the CT, most of the D-neutral amino acids produced significantly larger responses in the GSP than did the L-neutral amino acids. These results suggest that the strong stimulatory effectiveness induced by D-neutral amino acids in the rat GSP depend not only on the strong responsiveness to sweet substances but also on the different stimulatory effectiveness for neutral amino acid.

During the first 8 weeks of development in the rat, the magnitude of the CT responses to 0.1 M NaCl increased. Responses to 0.01 M HCl and 0.01 M quinine-HCl (QHCl) were rather unstable until 3 weeks of age (Harada and Maeda, 2004). Response to sucrose increase and reached maximum at three weeks, then continuously decrease until 8 weeks of age. The relative integrated response magnitudes to all six 0.5 M sugars increased from 1 and 3 weeks of age, reaching a maximum at 3 weeks. At this age, the response magnitude to sucrose (Suc) and fructose (Fru) were significantly larger than those to the other sugars. After reaching a maximum, the response magnitude decreased until week 8. This latter decline in the response to sugars cannot be explained by an increase in the taste response to 0.1 M NH₄Cl since the response magnitude to 0.01 M HCl and QHCl did not decrease during the same time period.

It is plausible that the decrease of the sugar response was caused by a decrease in the number of sugar sensitive fibers or the number of receptor sites on the respective taste cells within the taste buds. On the other hand, the concentration–response relationships for Suc and maltose (Mal) did not differ in 14- to 35-day-old hamsters, while they increased in 55- to 73-day-old adult hamsters (Hill, 1988). High responsiveness to the sugars in the rat GSP (Hill, 1988; Harada and Smith, 1992; Harada *et al.*, 1994, 1997) could compensate for the decrease in responsiveness in the CT. Also, the different responses to sugars in the CT in the rat (Harada and Maeda, 2004) and hamster (Hill, 1988) may produce different developmental changes of sugar responsiveness observed between the two species.

The results of the cross adaptation experiment in the rat at 1 and 8 weeks of age suggested that there might be individual sugar receptors on the taste buds innervated by the CT of the adult rat even at the early postnatal age of 2 weeks (Harada and Maeda, 2004). This result indicated that different sugar receptors arise at an early stage

in development and facilitate the ability of the rat pup to distinguish the taste of sugars during suckling behavior.

Finally, just after birth, gustatory information from the GSP may play an important role for the newborn rat pup, then within one to two weeks after birth, information from the CT rapidly increases and may modify the feeding behavior. Then, the importance of the information from the glossopharyngeal nerve may increase later of the preweanling period.

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