1. INTRODUCTION

The morphological and functional development of the rat gustatory system occurs primarily postnatally. As such, stimulus-induced processes likely play a major role in organizing the sense of taste. However, some very important events that direct development occur long before the gustatory system becomes functional. In order to examine some of the very early organizational processes, it has been necessary to institute experimental manipulations prenatally and then examine the effects as the system develops. Thus, by relating the neurobiological effects with prenatal manipulations, it is the hope that we can get a picture of events that serve to shape the long-term organization of the system during normal development. Moreover, as with all other sensory systems, it is important to identify processes that may have long-term (or permanent) detrimental effects on sensory and brain development. It is my goal in this chapter to provide background information about normal gustatory development that provides the necessary standard by which experimentally induced alterations can be compared, and to then describe findings resulting from early environmental manipulations.

2. NORMAL DEVELOPMENT OF THE GUSTATORY SYSTEM

2.1. Peripheral Functional Development

Neurophysiological taste responses change in a progressive and orderly manner throughout a prolonged period of the rat’s postnatal development. In the peripheral gustatory system, chorda tympani nerve taste responses can be recorded as early as two days postnatal (Hill and Almli, 1980). However, response magnitudes to monochloride salt increase dramatically during the first three weeks after birth (Ferrell, Mistretta, and Bradley, 1981; Hill and Almli, 1980; Yamada, 1980). Specifically, response frequencies of
single chorda tympani fibers to NaCl and LiCl increase while frequencies to NH₄Cl remain constant (Hill, Mistretta, and Bradley, 1982). Interestingly, response frequencies to citric acid decrease throughout development. Thus, the peripheral gustatory system is capable of responding in a mature manner to some stimuli (e.g., NH₄Cl) as soon it becomes functional, but changes in its sensitivity to others (e.g., NaCl) during an extended developmental period (Fig. 1).

The cellular mechanisms responsible for the increase in peripheral response frequencies to NaCl relate to the addition of functional taste receptor membrane components that are sensitive to the epithelial sodium transport blocker, amiloride (Hill and Bour, 1985) (Fig. 1). This sodium transporting channel has been characterized in other epithelia (Garty and Benos, 1988), and has been implicated as the major, if not only membrane component mediating salt taste transduction in the rat (Avenet and Lindemann, 1988; DeSimone and Ferrell, 1985; Formaker and Hill, 1988; Hill, Formaker, and White, 1990; Ye, Heck, and DeSimone, 1991). Recent experiments that combine in vivo voltage clamp with whole nerve electrophysiological recordings from the chorda tympani nerve have provided further evidence of increased sodium transduction pathways during development. Briefly, the voltage applied across the lingual epithelia is clamped at positive or negative voltage, thereby decreasing or increasing the driving force, respectively, for sodium to enter the taste receptor cell. By simultaneously recording from the nerve, it is possible to examine the consequences of the voltage clamp during salt stimulation and to derive biophysical measures of receptor channel density and efficiency (Stewart, Hendricks, Heck, DeSimone, and Hill, 1997). These experiments reveal that there are dramatic increases in the numbers of functional amiloride sensitive sodium channels that are located in the apical portion of taste receptor cells (i.e., the area most likely to contact gustatory stimuli). Specifically, the combined neurophysiological and biophysical analyses show that there are approximately 19%, 44%, and 85% of functional amiloride channels in rats aged 10–14 days, 19–23 days, and 29–31 days, respectively, compared to adults.

Interestingly, immunocytochemical and whole cell patch clamp evidence suggests that at least part of the amiloride-sensitive channel is present in rat fungiform taste buds at birth (Stewart, Lasiter, Benos, and Hill, 1997). Immuno-positive labeling with a polyclonal antibody directed at the epithelial sodium channel (ENaC) is evident in taste buds beginning in 1-day-old rats and are qualitatively unchanged throughout development.

**Figure 1.** Time scale showing important events in the functional and morphological development of the peripheral gustatory system. CT—chorda tympani nerve.