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Research Report

Rewiring the gustatory system: Specificity between nerve and taste bud field is critical for normal salt discrimination

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ABSTRACT

Forty years have passed since it was demonstrated that a cross-regenerated gustatory nerve in the rat tongue adopts the stimulus–response properties of the taste receptor field it cross-reinnervates. Nevertheless, the functional consequences of channeling peripheral taste signals through inappropriate central circuits remain relatively unexplored. Here we tested whether histologically confirmed cross-regeneration of the chorda tympani nerve (CT) into the posterior tongue in the absence of the glossopharyngeal nerve (GL) (CT-PostTongue) or cross-regeneration of the GL into the anterior tongue in the absence of the CT (GL-AntTongue) would maintain presurgically trained performance in an operant NaCl vs. KCl taste discrimination task in rats. Before surgery all groups were averaging over 90% accuracy. Oral amiloride treatment dropped performance to virtually chance levels. During the first week after surgery, sham-operated rats, GL-transected rats, and rats with regenerated CTs displayed highly competent discrimination performance. In contrast, CT-transected rats were severely impaired (59% accuracy). Both the CT-PostTongue and the GL-AntTongue groups were impaired to a similar degree as CT-transected rats. These initially impaired groups improved their performance over the weeks of postsurgical testing, suggesting that the rats were capable of relearning the task with discriminable signals in the remaining taste nerves. This relearned performance was dependent on input from amiloride-sensitive receptors likely in the palate. Overall, these results suggest that normal competence in a salt discrimination task is dependent on the taste receptor field origin of the input as well as the specific nerve transmitting the signals to its associated circuits in the brain.

1. Introduction

The rodent gustatory system represents an excellent experimental platform for studying neural plasticity and its functional concomitants. Taste bud cells have limited life spans on the order of about 10 days and are routinely replaced by perigemmal progenitor cells (Beidler and Smallman, 1965; Farbman, 1980). This means that new synapses are constantly being formed. Moreover, taste buds, which degenerate upon interruption of the nerve supply, reappear when a transected lingual taste nerve regenerates and reinnervates its native receptor field (see Barry and Frank, 1992). Notably, for the most part, taste functions that are disrupted upon nerve transection are restored once the nerve successfully reinnervates its normal epithelial region (Barry et al., 1993; Cain et al., 1996; St. John et al., 1995; King et al., 2000; Kopka et al., 2000; Kopka

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and Spector, 2001; Yasumatsu et al., 2003; Geran et al., 2004). For the chorda tympani nerve (CT), this recovery of function occurs despite the seemingly permanent anatomical alterations in the gustatory system following regeneration including: decreases in the number of anterior tongue taste buds and their volume (Shuler et al., 2004), decreases in the number of myelinated fibers in the regenerated CT coupled with decreased number of cell bodies in the geniculate ganglion (Cain et al., 1996) and reduced volume and density of the CT terminal projection field in the nucleus of the solitary tract (Barry, 1999).

One of the truly remarkable characteristics of the peripheral gustatory system, at least in rodents, is that the lingual taste nerves can be surgically cross-wired (Oakley, 1967a,b, 1995; Ninomiya, 1998; Smith et al., 1999; King et al., 2008). This provokes questions regarding the functional consequences of cross-regeneration. Relatively little has been done to examine this behaviorally. Several decades ago, Oakley (1969) demonstrated that rats surprisingly displayed normal preference–aversion functions in long-term two-bottle tests after the glossopharyngeal nerve (GL), which normally innervates taste buds in the posterior tongue, was cross-regenerated into the anterior tongue on one side and the remaining lingual taste receptor fields were left denervated. These tests, however, are not optimal for testing gustatory function. In fact, completely denervating the taste buds on the tongue has limited effects on such measures (see Spector, 2003).

In order to approach the question of whether animals with cross-regenerated taste nerves are functionally competent, it is critical that two conditions be met. First, a taste-related behavior that is unequivocally disrupted by transection of one lingual gustatory nerve but not by the other must be used in the experimental design. Second, any transection-induced disruptions in behavior must recover upon normal regeneration of the nerve. Recently, King et al. (2008) conducted an experiment that satisfied these two conditions. Gaping, a hallmark taste-elicited oral motor rejection response, is severely disrupted by GL but not CT transection (Travers et al., 1987; Grill et al., 1992; King et al., 1999, 2000). The response is restored upon normal regeneration of the GL (King et al., 2000). King et al. (2008) found that quinine-induced gaping was normal in rats that had the posterior tongue taste buds cross-reinnervated by the CT with the anterior tongue taste buds left denervated. In contrast, rats that had the anterior tongue taste buds reinnervated by the GL with the posterior tongue taste buds left denervated were severely impaired. Thus, in this particular case, the receptor field reinnervated appeared to be the critical variable, not the nerve transmitting the signals to the brain.

In this paper, we focus on the effects of cross-regeneration of the CT and GL on salt taste discrimination performance in rats. Operantly conditioned performance on such tasks, while high presurgically, is severely disrupted by CT transection but is entirely unaffected by GL transection (Spector and Grill, 1992; St. John et al., 1995; Kopka et al., 2000). When the CT regenerates, performance returns to normal. The experiment reported here examined whether the recovery of function upon reinnervation of the anterior tongue taste buds is dependent on the reinnervating nerve, the reinnervated field of taste receptors, or both.

2. Results

Before surgery all of the rats performed the salt discrimination task extremely well and there were no differences among the groups in their percentage correct across all trials collapsed across stimuli and concentrations ($F(6,26)=0.46$, $p=0.835$; Fig. 1). As expected, when the epithelial sodium channel (ENaC) blocker amiloride, which suppresses the sodium-specific taste transduction pathway in rodents, was used as the solvent,

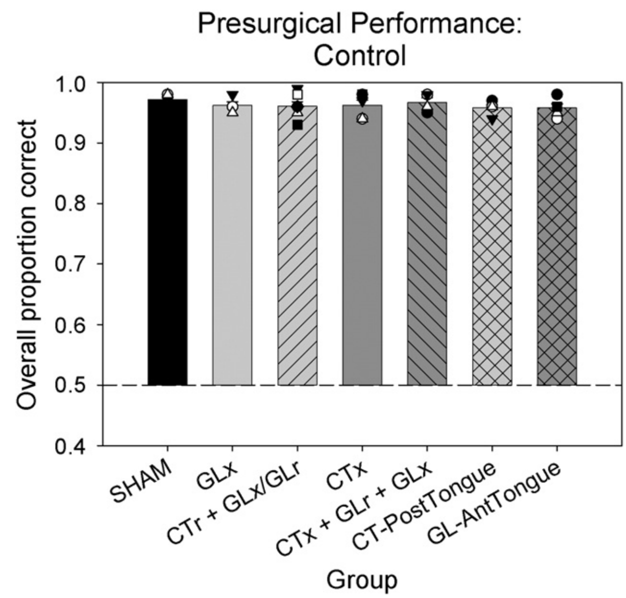

Fig. 1 – The mean (±SE) overall proportion correct on the NaCl vs. KCl discrimination task collapsed across all NaCl and KCl trials on the last six presurgical test sessions without amiloride treatment. The different symbols represent the performance of individual rats and are consistent within a specified group across all figures. It is clear that all of the groups were displaying high levels of performance in the task before surgery. SHAM: Sham-operated controls; GLx: permanent bilateral transection of the glossopharyngeal nerve; CTr + GLx/GLr: bilateral regeneration of the chorda tympani nerve coupled with either bilateral regeneration of the glossopharyngeal nerve or permanent bilateral transection of the glossopharyngeal nerve; CTx: permanent bilateral transection of the chorda tympani nerve; CTx + GLr + GLx: unilateral regeneration of the glossopharyngeal nerve coupled with contralateral permanent transection of the glossopharyngeal nerve and permanent bilateral transection of the chorda tympani nerve; CT-PostTongue: bilateral cross anastomoses of the central portion of the chorda tympani nerve with the peripheral portion of the glossopharyngeal nerve resulting in bilateral reinnervation of the posterior tongue taste buds by the chorda tympani nerve coupled with lack of taste nerve innervation of the anterior tongue; GL-AntTongue: bilateral cross anastomoses of the central portion of the glossopharyngeal nerve with the peripheral portion of the chorda tympani nerve resulting in bilateral reinnervation of the anterior tongue taste buds by the glossopharyngeal nerve coupled with lack of taste nerve innervation of the posterior tongue.