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BRAIN RESEARCH

Research Report

# Effects of electrical stimulation of the glossopharyngeal nerve on cells in the nucleus of the solitary tract of the rat

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ABSTRACT

Electrophysiological responses to electrical stimulation of the lingual branch of the glossopharyngeal (GP) nerve (which innervates taste buds on the caudal 1/3 of the tongue) were recorded from single cells in the rostral nucleus of the solitary tract (NTS) of anesthetized rats. Electrical stimulation was delivered as single pulses ($n=55$), paired-pulses ($n=15$) and tetanic trains ($n=11$). NTS cells with GP-evoked responses were also tested for responsivity to taste stimuli (0.1 M NaCl, 0.5 M sucrose, 0.01 M HCl and 0.01 M quinine HCl). Fifty-five neurons were studied: 49 cells showed GP-evoked (mean latency ± SEM = 18.0 ± 1.32 ms); seven of these were taste-responsive. Spontaneous rate of these cells was low (mean ± SEM = 1.4 ± 0.3 spikes per second; median = 0.21 spikes per second) and many cells showed no spontaneous activity. Paired-pulse stimulation of the GP nerve in 13 rats produced both paired-pulse suppression ($n=11$) and paired-pulse enhancement ($n=4$); tetanic stimulation (25 Hz, 1.0 s) produced sustained (>20 s) increases or decreases in firing rate in 7 of 11 cells tested. Histological data suggested that GP-evoked responses recorded in the most rostral NTS were likely the result of polysynaptic connections. Cells with GP-evoked responses formed a heterogeneous group in terms of their response properties and differed from cells with evoked responses to chorda tympani (CT; which innervates taste buds on the rostral 1/3 of the tongue) nerve stimulation. These differences may reflect the respective functional specializations of the GP and CT nerves.



## 1. Introduction

The primary function of the taste system is to mediate the ingestion of nutrients and the rejection of potential poisons. This task involves the perception of taste stimuli as well as the command and modulation of orofacial reflexes. Previous research has shown that both the perception of a tastant and the orchestration of an appropriate oromotor reaction to it can be accomplished wholly within the brainstem, without the benefit of forebrain input or feedback (Grill and Norgren, 1978). Thus, an appreciation of the brainstem neural circuitry by which gustatory stimuli are processed and which drives orofacial motor output is essential for a complete understanding of the ingestive process. Of the three cranial nerves that innervate the taste buds of the oropharyngeal area, the glossopharyngeal (GP) nerve (IX) is thought to sustain orofacial gestures, particularly those associated with aversive tastants, while the facial nerve (VII) is thought to play a critical role in taste discrimination. Though the GP nerve innervates over two thirds of the taste buds in oropharyngeal area (Spector and

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Grill, 1992), Frank (1991) has argued that there is insufficient information contained in the responses of GP nerve fibers to account for taste discrimination. Subsequently, it was demonstrated that transection of the GP nerve significantly impairs orofacial reactivity to aversive taste stimuli (Grill et al., 1992; King et al., 1999; Travers et al., 1987), and that GP nerve transection has a relatively minor effect on taste thresholds or discrimination (Spector and Grill, 1992; Spector et al., 1997; St. John and Spector, 1998).

In the central nervous system, the nucleus of the solitary tract (NTS) serves as the first site for the integration and interpretation of gustatory information from the tongue. In mammals, the facial and GP nerves send gustatory information from the tongue to the rostral NTS where they terminate in a roughly topographical, though partially overlapping, distribution (Hamilton and Norgren, 1984; Travers et al., 1986). Anatomical (Hamilton and Norgren, 1984) and physiological (Travers and Norgren, 1995) studies have shown that the GP-NTS projection is restricted largely to the caudal portion of the rostral, taste-responsive portion of the NTS. However, cutting the GP nerve eliminates c-*fos*-labeled cells located throughout the rostrocaudal extent of the NTS following intraoral infusions of quinine in rats (Harrer and Travers, 1996; King et al., 1999), suggesting a more widespread terminal distribution of GP fibers. Since cutting the GP nerve also severely impairs aversive taste reactivity to quinine, a bitter tastant, it is likely that NTS cells receiving direct GP nerve input participate in the initiation and/or modulation of these behaviors.

In the present experiment, our goals were twofold. First, we wanted to identify the location of NTS cells with GP-evoked responses. Based on studies using c-*fos*, cited above, our hypothesis was that we would find these cells scattered throughout the rostrocaudal extent of the taste-responsive portion of the NTS. Second, we wanted to characterize the electrophysiological responses to electrical stimulation of the GP nerve in NTS cells. We identified cells that could be driven by GP stimulation by exploring the taste-responsive portion of the NTS while electrically stimulating the GP nerve. Once identified, we tested these cells with a number of experimental protocols in an effort to discover the type and parameters of stimuli that were most effective in driving them. Specifically, these included taste stimuli and electrical stimulation in the form of single pulses, paired-pulses and tetanic trains. This paradigm parallels a previous study of the effects of electrical stimulation of the chorda tympani (CT; a branch of the facial nerve innervating taste buds on the rostral 2/3 of the tongue) nerve on cells in the NTS (Lemon and Di Lorenzo, 2002). In that study, it was suggested that afferent volleys from the CT nerve generate inhibitory activity with a time course of ~1 s. Whether NTS cells with GP-evoked responses are also subject to this type of influence was investigated here. We also tested the effects of a brief tetanic pulse train on the firing characteristics of these cells.

## 2. Results

Electrophysiological responses to tastants and to electrical stimulation of the GP nerve were recorded in 55 single cells in the NTS. There were 49 cells that showed evoked responses to GP nerve stimulation; seven (14%) of these responded to taste stimulation. The remaining six cells were taste-responsive cells that did not show an evoked response to GP nerve stimulation, but were recorded in preparations where a GP-evoked response was present in other cells. All of these cells were recorded in or near an area of the brainstem where background responses to taste stimuli were present. Specifically, in addition to the seven taste-responsive cells, 28 cells with GP-evoked responses (57%) were recorded at positions where background taste responses were apparent, even though the recorded cell did not respond to taste stimuli. The remaining 14 cells (29%) were recorded at sites where no background responses were apparent, but where taste responses could be detected in other electrode penetrations within a radius of 200–300 μM. Taste-responsive cells that did not respond to GP nerve stimulation were only recorded after collecting data from cells that did show GP-evoked responses. That is, we did not make an effort to isolate or record from taste-responsive cells that did not show evoked responses to GP nerve stimulation. Thus, the taste-responsive cells without GP-evoked responses in the present study are only a small sample of such cells in this portion of the NTS.

Cells that responded to GP nerve stimulation generally showed little or no spontaneous activity. The average spontaneous rate of these cells (mean ± SEM) was 1.42 ± 0.30 sps (median = 0.21 sps). The spontaneous rate of non-taste-responsive cells ($n$ = 40; 1.15 ± 0.31 sps) was significantly

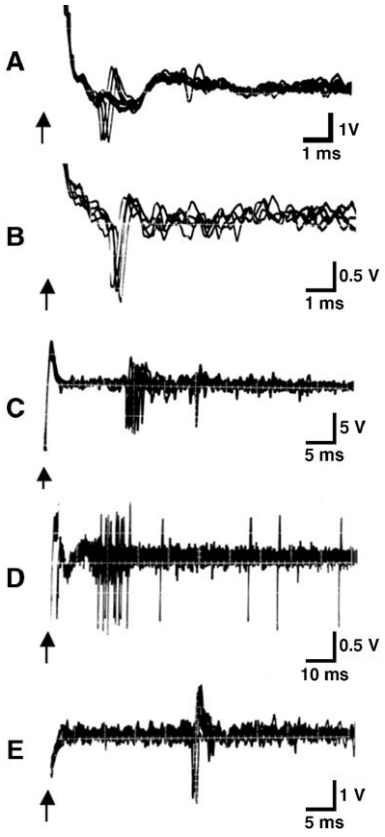


**Fig. 1 – (A–E) Oscilloscope tracings from five representative NTS cells showing evoked responses to GP nerve stimulation. Each panel shows 5–10 sweeps superimposed.**