

Research report

Effect of peripherally and cortically evoked swallows on jaw reflex responses in anesthetized rabbits

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ABSTRACT

This study aimed to investigate whether the jaw-opening (JOR) and jaw-closing reflexes (JCR) are modulated during not only peripherally, but also centrally, evoked swallowing. Experiments were carried out on 24 adult male Japanese white rabbits. JORs were evoked by trigeminal stimulation at 1 Hz for 30 s. In the middle 10 s, either the superior laryngeal nerve (SLN) or cortical swallowing area (Cx) was simultaneously stimulated to evoke swallowing. The peak-to-peak JOR amplitude was reduced during the middle and late 10-s periods (i.e., during and after SLN or Cx stimulation), and the reduction was dependent on the current intensity of SLN/Cx stimulation: greater SLN/Cx stimulus current resulted in greater JOR inhibition. The reduction rate was significantly greater during Cx stimulation than during SLN stimulation. The amplitude returned to baseline 2 min after 10-s SLN/Cx stimulation. The effect of co-stimulation of SLN and Cx was significantly greater than that of SLN stimulation alone. There were no significant differences in any parameters of the JCR between conditions. These results clearly showed that JOR responses were significantly suppressed, not only during peripherally evoked swallowing but also during centrally evoked swallowing, and that the inhibitory effect is likely to be larger during centrally compared with peripherally evoked swallowing. The functional implications of these results are discussed.

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1. Introduction

Ingestion is the early stage of nutrition in most mammals. It is widely accepted that masticatory movements, including chewing and swallowing, are programmed by the central nervous system, including a central pattern generator (CPG) in the brainstem (Jean, 2001; Miller, 1982; Nakamura and Katakura, 1995).

Swallowing can be triggered by either peripheral or central inputs (Jean, 2001). For the former, pharyngeal and laryngeal stimulation can readily evoke the swallowing reflex. Electrical stimulation of the superior laryngeal nerve (SLN), which contains the pharyngeal/laryngeal sensory nerve, is one of the most common methods for activating the swallowing CPG in animals (Jean,

2001) and in humans (Aida et al., 2015; Tsukano et al., 2012). Brain imaging studies have shown that some cortical loci are involved in the voluntary swallowing process in humans, including the sensorimotor cortex, primary sensory cortex, inferior parietal lobe, insula, and anterior cingulate cortex, although there is some variability between studies (see (Humbert and Robbins, 2007; Soros et al., 2009)). Although a number of studies have corroborated neurophysiological data in animals (Martin and Sessle, 1993; Martin et al., 1997; Martin et al., 1999; Narita et al., 1999) and humans (Hiraoka, 2004), some contradictory results have been reported. For example, some studies reported laterality of sensorimotor cortical activation (Dziewas et al., 2003; Martin et al., 2004; Teismann et al., 2009) while others revealed bilateral activation (Hamdy et al., 1999b; Zald and Pardo, 1999). Furthermore, the location of insula activation has varied between studies, with some studies reporting left insula (Dziewas et al., 2003), right insula (Martin et al., 2001), anterior insula (Hamdy et al., 1999a), or posterior insula (Suzuki et al., 2003) activation. This discrepancy may be due to differences in the swallowing tasks used (voluntary or reflexive swallowing; bolus or saliva swallowing) and/or the demographics of the participants.

Abbreviations: CPG, central pattern generator; Cx, cortical swallowing area; Dig, digastric muscle; EMG, electromyography; IAN, inferior alveolar nerve; JCR, jaw-closing reflex; JOR, jaw-opening reflex; Mas, masseter muscle; MesV, mesencephalic trigeminal nucleus; SLN, superior laryngeal nerve; Thy, thyrohyoid muscle.

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Recently, we succeeded in initiating swallowing by electrical stimulation of the swallowing cortical area (Cx) within the insular cortex in anesthetized rats (Tsujiura et al., 2016). In this study, we found that the onset latency of the first swallow evoked by insular stimulation was significantly longer than that evoked by stimulation of the SLN. These results might be expected because initiating centrally evoked swallowing in natural situations involves activation of not only the insular cortex but also other areas, as described above.

It has been reported that the jaw-opening reflex (JOR), one of the elementary jaw reflexes evoked by trigeminal stimulation (Lund et al., 1981; Lund et al., 1983), is suppressed during chewing. The finding that paralysis does not change such modulation, in which the excitability of the JOR pathway is modulated during chewing, strongly suggests that these processes are not dependent on the sensory feedback system (Lund et al., 1983).

Our previous studies revealed that the JOR is suppressed not only during chewing but also during swallowing. Yamada et al. (Yamada et al., 2013) reported that JOR evoked by innocuous intra-oral stimulation was suppressed during natural chewing and swallowing in conscious animals. Fukuhara et al. (Fukuhara et al., 2011) investigated the effects of swallowing responses evoked by electrical stimulation of the SLN on JORs in anesthetized animals. The authors found that JORs evoked by low-threshold trigeminal afferents were significantly inhibited during and after SLN stimulation. This suggested that activation of the swallowing-related neural network, but not the swallowing movements, is involved in the inhibition of JORs. Such processes may be required to prevent undesirable jaw movements caused by weak stimulation during functions such as chewing and swallowing.

The present study aimed to investigate whether JOR responses are modulated not only during peripherally evoked swallowing but also during centrally evoked swallowing. In addition, changes in the opposing jaw reflex (i.e., jaw-closing reflex; JCR) during swallowing, were also investigated. We hypothesized that JORs would be inhibited not only by peripheral inputs but also central inputs to evoke swallowing, and that the stimulus intensity applied to the central and peripheral regions to evoke swallowing would be similarly related to the reduction of JORs.

2. Results

2.1. Baseline data

The inferior alveolar nerve (IAN) stimulus threshold to evoke the JOR in the digastric (Dig) muscle ranged from 0.05 to 0.30 mA (0.12 ± 0.07 mA, $n = 30$) and that of the mesencephalic trigem-

inal nucleus (MesV) to evoke the JCR in the masseter (Mas) muscle ranged from 0.02 to 2.00 mA (0.53 ± 0.49 mA, $n = 14$). The onset latency of the JOR ranged from 6.42 to 9.64 ms (7.62 ± 0.77 ms, $n = 30$) and that of the JCR ranged from 1.71 to 2.18 ms (1.96 ± 0.13 ms, $n = 13$).

The SLN stimulus threshold ranged from 0.02 to 0.60 mA (0.10 ± 0.12 mA, $n = 31$) and that of Cx ranged from 0.10 to 2.00 mA (1.03 ± 0.63 mA, $n = 29$). The mean number of swallows evoked by SLN stimulation increased and onset latency of the first swallow decreased with increasing stimulus intensity (Fig. 1). This was not the case for Cx stimulation; there was no difference in the number of swallows and the onset latency of the first swallow with Cx stimulation between 1.0 and 1.4 times (T) the threshold for eliciting the swallowing reflex at least once for 10 s (Fig. 1).

2.2. Effect of SLN/Cx stimulation on JORs

An example JOR recording is shown in Fig. 2. JOR responses, in terms of peak-to-peak amplitude, were inhibited during and immediately after swallowing evoked by SLN and Cx stimulation. The mean JOR amplitude was significantly smaller in the middle and late 10-s periods (i.e., during and after SLN/Cx stimulation) compared with the early 10-s period (i.e., before SLN/Cx stimulation) (Fig. 3). The inhibitory effect on the JORs was dependent on the stimulus intensity, such that greater SLN/Cx stimulus intensity was associated with greater inhibition. There was no difference in the reduction rate of JOR amplitude between ipsilateral and contralateral SLN/Cx stimulation and the latency among the stimulus conditions of SLN/Cx (data not shown).

Time-dependent changes in JOR responses were analyzed (Fig. 4). The JOR amplitude gradually decreased during SLN/Cx stimulation and continued to decrease after stimulation, returning to baseline level (i.e., before SLN/Cx stimulation) 2 min after SLN/Cx stimulation.

To evaluate how the occurrence of swallowing is related to the inhibition of JOR responses and to compare SLN and Cx stimulation, we calculated the reduction rate of JOR amplitude per swallow (Fig. 5). The rate was significantly greater during Cx stimulation at 1.0 T than during SLN stimulation at 1.0 T.

2.3. Effect of co-stimulation of SLN and Cx on JORs

JOR responses were strongly inhibited during co-stimulation of SLN and Cx. JOR amplitude was significantly smaller during co-stimulation of SLN and Cx than during SLN (4.0 T) stimulation alone, but not significantly smaller than that during Cx (1.0 T) stimulation alone (Fig. 6).

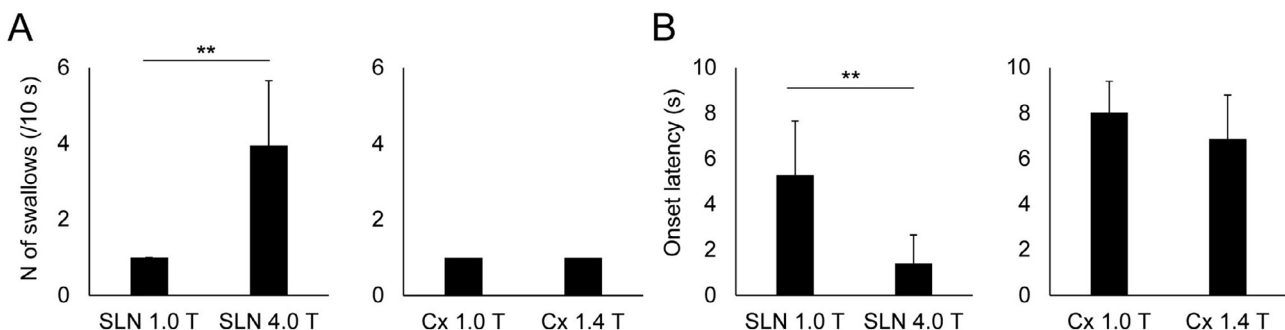


Fig. 1. The number of swallows and onset latency of the first swallow during SLN/Cx stimulation. A: The number of swallows during 1.0 T and 4.0 T SLN stimulation was 1.0 ± 0.0 and 4.0 ± 1.7 ($n = 22$ for each group), respectively, and that during 1.0 and 1.4 T Cx stimulation was 1.0 ± 0.0 and 1.0 ± 0.0 ($n = 17$ for each group), respectively. B: The onset latency of the first swallow during 1.0 T and 4.0 T SLN stimulation was 5.3 ± 2.4 s and 1.4 ± 1.3 s ($n = 22$ for each group), respectively, and that during 1.0 and 1.4 T Cx stimulation was 8.0 ± 1.4 s and 6.9 ± 1.9 s ($n = 17$ for each group), respectively. During 0.8 T SLN/Cx stimulation, no swallows were evoked in any of the animals. $^{**}p < 0.01$.

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