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Research Report

Differential involvement of two cortical masticatory areas in submandibular salivary secretion in rats

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ABSTRACT

To evaluate the role of the masticatory area in the cerebral cortex in the masticatory-salivary reflex, we investigated submandibular salivary secretion, jaw-movement trajectory and electromyographic activity of the jaw-opener (digastric) and jaw-closer (masseter) muscles evoked by repetitive electrical stimulation of the cortical masticatory area in anesthetized rats. Rats have two cortical masticatory areas: the anterior area (A-area) in the orofacial motor cortex, and the posterior area (P-area) in the insular cortex. Our defined P-area extended more caudally than the previous reported one. P-area stimulation induced vigorous salivary secretion (about 20 μl/min) and rhythmical jaw movements (3–4 Hz) resembling masticatory movements. Salivary flow persisted even after minimizing jaw movements by curarization. A-area stimulation induced small and fast rhythmical jaw movements (6–8 Hz) resembling licking of solutions, but not salivary secretion. These findings suggest that P-area controls salivary secretion as well as mastication, and may be involved in the masticatory-salivary reflex.

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1. Introduction

Profuse saliva is secreted during feeding, which is known as the masticatory-salivary reflex and/or gustatory-salivary reflex. The reflexes are initiated and maintained by various oral sensory afferents, including mechanoreceptors in the periodontal membrane and gingivae, and taste bud activation (for review, see Hector and Linden, 1999). Electrophysiological studies show that the fundamental neural substrate subserving the reflexes exists in the lower brainstem, since in decerebrate animals multiple oral sensory inputs can evoke salivation and neural activity of the autonomic nerves innervating the salivary glands (Kawamura and Yamamoto, 1978; Matsuo and Yamamoto, 1989; Matsuo et al., 1989). On the other hand, feeding behavior is under the control of forebrain areas such as the lateral hypothalamic area (feeding center), central nucleus of the amygdala (relates to taste processing), and cerebral cortex (gustatory area or part of masticatory area). Electrical stimulation of these structures activates parasympathetic preganglionic neurons (secretory neurons) to the submandibular gland in anesthetized rats (Matsuo, 1999a; Matsuo and Kusano, 1984) and cats (Ishizuka and

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Murakami, 1989). Moreover, such stimulation modifies taste responses in the nucleus of the solitary tract (the first central taste relay) and parabrachial nucleus (the second central taste relay) in rats (Lundy and Norgren, 2004; Matsuo et al., 1984) and hamsters (Cho et al., 2003; Li et al., 2005). These findings suggest that a role of the forebrain is the modification of the salivary reflexes being processed in the lower brainstem, and/or that the cerebral cortex may be involved in the neural circuit of salivary reflexes.

Early studies suggest that the cerebral cortex, of which electrical stimulation evokes vigorous salivation, corresponds with the masticatory area in dogs (Babkin and Van Buren, 1951) and cats (Hess et al., 1952) and the gustatory area in dogs (Funakoshi, 1972) and rats (Yamamoto, 1999). However, more recent studies have shown that the masticatory cortex consists of two or more separate regions. For example, two and four cortical areas have been identified in rats (Sasamoto et al., 1990) and monkeys (Huang et al., 1989), respectively, and rabbits have wide and overlapping cortical areas, of which electrical stimulation produces several patterns and rhythms of jaw movements (Liu et al., 1993; Lund et al., 1984). In spite of the different motor functions of the masticatory cortices, their corticofugal effects on salivary secretion or salivary reflexes have not been investigated yet.

In the present study, we analyzed jaw movements and submandibular salivary secretion induced by intracortical microstimulation applied to the cerebral cortex including the two masticatory areas in rats. One masticatory area (A-area) is situated in the orofacial motor cortex, of which electrical stimulation produces small vertical opening–closing jaw movements with high frequency of 5–7 Hz. The other area (P-area) overlaps the gustatory area in the insular cortex, of which stimulation induces large and complex lateral and vertical movements with low frequency of 3–4 Hz (Sasamoto et al., 1990; Zhang and Sasamoto, 1990). There is a sparse reciprocal connection between the two cortical areas, suggesting that they work independently (Zhang and Sasamoto, 1990). Recent studies have shown differential corticofugal effects of the two masticatory areas on the swallowing reflex (Tsujimura et al., 2012) and on modulation of rhythmical jaw movements by the red nucleus (Satoh et al., 2006, 2007). In addition to such functional differences, we here provide evidence that P-area, but not A-area, is related to salivation, and discuss the role of the masticatory cortex in the masticatory-salivary reflex.

2. Results

2.1. Stimulation site in the cerebral cortex

Rhythmical jaw movements were induced by repetitive electrical stimulation applied to the orofacial motor cortex and insular cortex, which include previously reported A-area and P-area (Sasamoto et al., 1990; Zhang and Sasamoto, 1990), respectively. However, our defined P-area extended caudally. As shown in Fig. 1, the stimulation sites in A-area ($n=13$) were grouped in the primary motor cortex (M1) about 3–4 mm rostral to the bregma according to the stereotaxic atlas by Paxinos and Watson (1998). The stimulation sites in P-area ($n=17$) were scattered in the granular (GI) and dysgranular (DI) insular cortex and the dorsal (AID) and posterior (AIP) parts of the agranular insular cortex from about 1 mm rostral to about 1.5 mm caudal to the bregma according to the stereotaxic atlas.

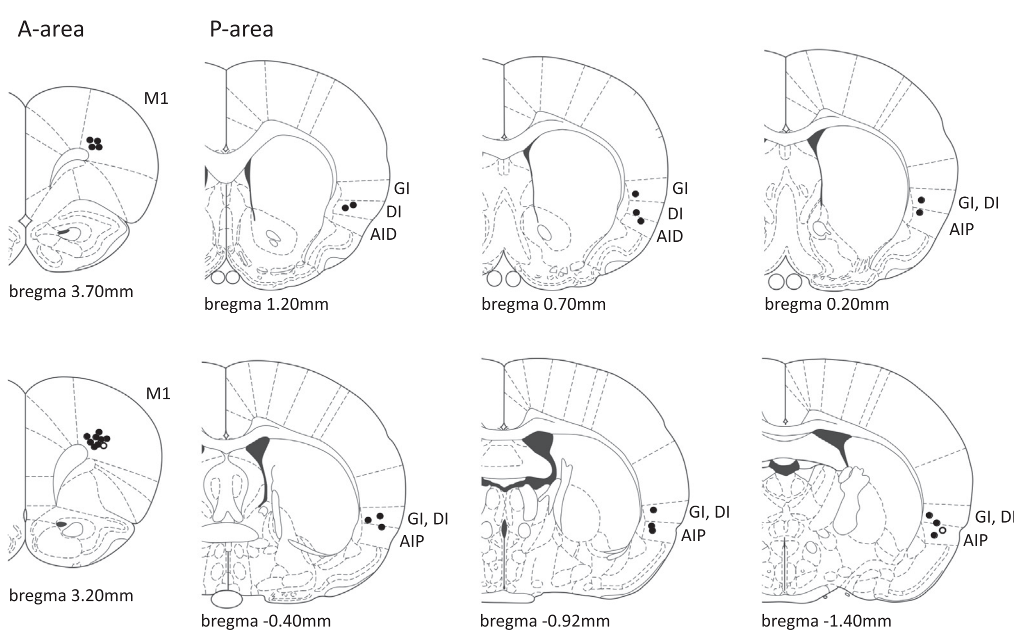

Fig. 1 – Schematic drawing of stimulation sites in the orofacial motor (A-area) and insular cortices (P-area) on the left side. Open circles at 3.20 mm and −1.40 mm from bregma indicate stimulation sites for Figs. 2 and 3, respectively. AID=dorsal part of the agranular insular cortex, AIP=posterior part of the agranular insular cortex, DI=dysgranular insular cortex, GI=granular insular cortex, and M1=primary motor cortex.

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