

Coordination of cranial motoneurons during mastication

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Abstract

Mastication is the first stage of digestion and involves several motor processes such as food intake, intra-oral food transport, bolus formation and chewing in its broad sense. These complicated motor functions can be accomplished by the well-coordinated activities in various cranial motoneurons innervating the jaw, hyoid, tongue and facial muscles. The brainstem masticatory central pattern generator plays a crucial role in generating basic activity patterns of these cranial motoneuron groups. However, descending inputs from higher brain (e.g., cerebral cortex) and mastication-generated peripheral sensory inputs also play important roles in modulating the activity pattern of each motoneuron so that the final motor outputs fit the environmental demand. In this review, we focus on the coordination of the trigeminal, facial and hypoglossal motoneurons during mastication. We first summarize findings showing the activity patterns of muscles innervated by these motoneurons during natural mastication, and then discuss the possible neural mechanisms underlying their coordinated activities during mastication.

Key words: mastication; coordination; trigeminal; facial; hypoglossal; jaw; tongue; feeding; accessory respiratory muscle

Introduction

Mastication, characterized by cyclic jaw movements and associated facial and tongue movements, is the first stage of digestion in most mammals. Its prime function is the breakdown of foodstuffs to a form suitable for subsequent swallowing. The principal masticatory organs are the teeth, and the secondary structures are the tongue, the lips, the cheeks and the mucosa of the hard palate and dentoalveolar structures (Dubner et al., 1978). The activation of jaw-closing muscles plays a major role in the mechanical reduction of food particle size by generating masticatory forces between the teeth. Muscles of the tongue, cheeks, and lips also play important roles in holding foodstuffs in between the teeth for maximum effect. Highly complicated, mastication occurs simultaneously with several other motor processes such as food intake, intra-oral food transport and bolus formation (Dubner et al., 1978; Thexton, 1992), and most of the muscles participating in mastication also play important roles in these various motor functions. In addition, some of the muscles involved in these motor functions are also known to be active during respiration, which can simultaneously occur during mastication, and are considered to be accessory respiratory muscles (Van Lunteren and Dick, 1997). The genioglossus (GG), innervated by the hypoglossal (XII) motoneurons, may be the most important and most extensively studied of these; this muscle shows activity during inspiration and plays an important role in preventing upper airway narrowing or collapse during inspiration (Lowe, 1980; Bartlet, 1986). Recently, special attention has been paid to this muscle, since the loss of GG tone may be responsible for the pathogenesis of obstructive sleep apnea. In addition to the GG, respiration-related activity is sometimes observed in other muscles participating in mastication such as the mylohyoid (Lowe and Sessle, 1973). Therefore, to accomplish mastication and the

simultaneously occurring motor functions, activities of the jaw, hyoid, tongue and peri-oral facial muscles, which are innervated by different groups of cranial motoneurons, must be well coordinated.

To elucidate how motoneuronal activity is coordinated during mastication, recordings of electromyographic (EMG) activities in the muscles, as the final and summated motor output of each motoneuron group, may be a good approach. In this review, we primarily focus on three cranial motoneurons: V, VII (facial) and XII. We first summarize findings obtained from awake animals and humans showing the activity patterns of muscles innervated by these motoneurons during natural mastication. Then, the possible neural mechanisms underlying their coordinated activities during mastication are discussed.

1. Muscles involved in masticatory movements

Since most of the electrophysiological data described in this article are EMG activities of the muscles innervated by V, VII and XII motoneurons, we briefly introduce the functional roles and motoneuronal origins of muscles involved in masticatory movements.

1.1. Muscles of the jaw

Jaw muscles are classified into jaw closers and jaw openers, and are innervated by V motoneurons except that the posterior belly of the digastric is innervated by VII motoneurons. Jaw closers and openers are generally antagonistic in their actions. The former include the masseter, temporalis and medial pterygoid, and the latter include the digastric, mylohyoid and lateral pterygoid. The lateral pterygoid is not a genuine jaw-opener since its contraction does not produce jaw opening; it is active during jaw

closing, protrusive movements and jaw opening and stabilizes the condylar head of the jaw or moves it forward and laterally. This diversity is due to independent actions of superior and inferior heads of the lateral pterygoid (Hiraba et al., 2000). The suprathyroid also is a jaw opener, whereas the infrathyroid stabilizes the hyoid bone when contractions of the suprathyroid produce jaw opening.

1.2. Muscles of the Tongue

Tongue muscles are innervated by XII motoneurons and contribute to the motility of the tongue. There are two groups of tongue muscles: intrinsic and extrinsic. Intrinsic muscles have no attachment to any bone, terminating either within each other or in external tongue muscles. Activities of these muscles contribute particularly to the infinite variety of tongue shapes, and are important in certain aspects of masticatory movements (e.g., food transport). However, the activity patterns of these muscles are still unknown due to the technical difficulties in recording the activities of each fiber group, since contamination of the activities of the different fiber groups is unavoidable when EMG electrodes are inserted into the tongue. In the case of neuronal recording from XII motoneurons, identification of the muscle origin is almost impossible. Extrinsic tongue muscles include the GG, styloglossus and hyoglossus. The action of these muscles is sometimes explained as a man lying in a hammock (tongue body) with its cords (extrinsic muscles) attached to trees (bones). Therefore, their activities contribute to the positioning of the tongue and in changing its shape. Based on their major action, extrinsic muscles are functionally divided into two groups: tongue protractors and tongue retractors. The GG is usually considered the main protractor. The styloglossus retracts and elevates the tongue. The hyoglossus retracts but also depresses the lateral border of the tongue (for details, see (Lowe, 1980)). In addition to the tongue

muscles, suprathyroid muscles such as the geniohyoid along with infrathyroid muscles such as the sternothyroid and thyrohyoid are innervated by XII motoneurons. These muscles aid in depressing and fixing the mandible, the hyoid bone and the larynx. Hiiemae and Crompton (1985) pointed out the importance of hyoid muscles in the control of tongue movements. They suggested that changes in the position of the tongue depends on movement of the hyoid (that is, tongue base) resulting from differential contraction of the hyoid muscle, whereas contribution of the extrinsic tongue muscles is relatively small.

1.3. Facial muscles

Muscles involved in this muscle group are innervated by VII motoneurons. The facial muscles have one bony origin in the facial skeleton. The action of these muscles changes the shape of facial skin, cheeks and lips. The buccinator and orbicularis oris are known to be active during mastication (Møller, 1966; Blanton et al., 1970; Schieppati et al., 1989; Takada et al., 1996; Ootaki et al., 2004); they act synergistically with the tongue in the placement of the food bolus.

2. Masticatory movements during natural mastication

Before reviewing the motor output patterns of cranial motoneurons during mastication, we summarize how mastication is conducted during natural feeding behavior. The masticatory sequence, as termed by Schwerz et al. (1989), is the whole set of movements from ingestion to swallowing. On the basis of jaw-movements and the related activity pattern of the jaw muscles, they divided the sequence of awake rabbits into three functionally different masticatory periods: preparatory series, reduction series and preswallowing series. Similar attempts have been carried out in rabbit (Morimoto et

al., 1985; Yamada and Yamamura, 1996; Masuda et al., 1997; Ootaki et al., 2004), mouse (Okayasu et al., 2003) and monkey (Narita et al., 2002; Yamamura et al., 2002). In these studies, the masticatory sequence has consistently been divided into three periods, and general observations of jaw muscle activities as well as the functional implications of each period have also been consistent among these studies.

Once food has been ingested, the preparatory series (Stage I (Morimoto et al., 1985; Masuda et al., 1997) or food preparatory period (Narita et al., 2002; Yamamura et al., 2002; Ootaki et al., 2004)) occurs (Fig. 1). During this period, food is aggregated and broken into chewable pieces, and is moved backward to molar teeth. In the case of the above studies, except those conducted in freely moving animals (Yamada and Yamamura, 1996; Okayasu et al., 2003), test foods were small enough to chew so during this period mainly aggregating and transporting food seemed to occur. Subsequently the reduction series (Stage IIa (Morimoto et al., 1985; Masuda et al., 1997) or rhythmic chewing period (Narita et al., 2002; Yamamura et al., 2002; Ootaki et al., 2004)) occurs (Fig. 1). Most breaking down of food occurs during this period (Lund, 1991). The movements in this period are often called “chewing cycles” (Hiiemae, 1978; Hiiemae and Palmer, 1999). Finally, the preswallowing series (Stage IIb (Morimoto et al., 1985; Masuda et al., 1997) or preswallow period (Narita et al., 2002; Yamamura et al., 2002; Ootaki et al., 2004)) occurs several cycles preceding the swallowing event (Fig. 1). During this period, chewed food is transported toward the pharyngeal region for swallowing to occur.

While the above studies classified the entire masticatory sequence based on the pattern of jaw movements and related jaw muscle EMG activities, Hiiemae and colleagues classified the masticatory sequence into three periods (stage I transport,

processing and stage II transport) based on the position of the food bolus relative to the intraoral structures by videofluorography (Franks et al., 1985; Hiiemae and Crompton, 1985; Hiiemae et al., 1995). Stage I transport is the period in which ingested food is transported to the molars, and may functionally correspond to the preparatory series. Processing is the period when food is chewed to make it “swallowable”, and functionally corresponds to the reduction series. Stage II transport is the period in which chewed food is transported from the oral cavity to the pharyngeal region and functionally corresponds to the preswallowing series. These studies also revealed that stage II transport commences during the processing. These findings are consistent with those in awake animals, that the so-called interposed swallow (McFarland and Lund, 1993; Naganuma et al., 2001), a swallow event inserted within chewing cycles, can occur during the reduction series (Fig. 1). Thus, it is clear that bolus formation and food transportation do indeed occur during this period, and probably when the transported food bolus exceeds a certain amount, swallowing is reflexively induced.

3. Activity patterns and coordination of muscles innervated by the V, VII and XII motoneurons during mastication

Research on orofacial motility, and the underlying neural regulatory mechanisms of mastication, has largely focused on jaw movements and related activities in the jaw muscles. This may be, at least partly, due to the technical difficulties in monitoring the motility of the tongue and/or other soft tissues during mastication. Most recent electrophysiological studies investigating the motility on the tongue and other orofacial soft tissues during mastication utilize jaw movements as related kinematical information.

In this section, we first describe the activity patterns of the jaw muscles innervated by V motoneurons in relation to jaw movements. The activity patterns of muscles innervated by VII or XII motoneurons, contributing to motility in the orofacial soft tissues, are then described for each masticatory period. When correlating the activities in these muscles and the resultant orofacial movements during mastication, the following characteristic features of masticatory movement need to be kept in mind. 1) Since the jaw and other orofacial organs (e.g., tongue) are midline structures, well-coordinated action of bilateral musculatures is mandatory for the required movement. 2) Movements in orofacial organs are not necessarily symmetrical during mastication. 3) When organs move laterally, considerable time differences are noted in the activities of bilateral musculature. 4) Most of the muscles innervated by VII or XII motoneurons have no or only one attachment to bone; the stabilization of one side of the muscle is particularly important for these muscles for the production of their effective actions.

3.1. Preparatory series (Stage I, food preparatory period)

Recordings of jaw movements along with EMG recordings of the jaw muscles during this period have been conducted in mouse (Okayasu et al., 2003), rabbit (Schwartz et al., 1989; Ootaki et al., 2004), monkey (Narita et al., 2002; Yamamura et al., 2002) and man (Mioche et al., 2002). From these observations, the characteristic features of jaw movements and related activity patterns of jaw muscles, which were consistent among species, have been determined. 1) Depression of the jaw from its resting position (i.e., jaw opening) is the initial motion in this period. 2) The lateral shift of the jaw in each cycle is generally smaller than in the subsequent reduction series. 3) The EMG activities of jaw closers during jaw-closing phase are generally small (Fig. 1).

Scant information is available regarding the coordination of cranial motoneurons during this period; detailed quantitative analyses of EMG activities (e.g., their temporal relationships) of muscles innervated by different cranial motoneurons, have been made only for jaw and tongue muscles of monkeys that were well-trained to perform mastication with their head fixed (Yamamura et al., 2002). Their findings that the synchronized activities in the jaw opener (digastric) and tongue protractor (GG) occur during this period is generally consistent with those obtained by cinephotography (Hiemae et al., 1995), showing that all parts of the tongue moved forwards during early opening, and backwards during late opening in monkey. Although the above findings suggest that there is a tight linkage between the activities of tongue and jaw muscles, this may not be the case between the facial and jaw muscles. Ootaki et al. (2004) conducted simultaneous recordings of facial and jaw muscles during this period in awake rabbits, and reported that the activity patterns of facial muscles during this period were quite variable between animals despite that those of jaw muscles and the resultant jaw movements were relatively consistent. Since the pattern of jaw movements during this period is somewhat variable among animals of the same species (Ootaki et al., 2004), the movements during this period may not be controlled automatically but in an acquired manner, and the descending control of the cerebral cortex is important during this period (discussed in the section 4).

3.2. Reduction series (Stage IIa or rhythmic chewing period)

This period is characterized by a stable chewing rhythm, and a high level of activity in jaw closers. There are interspecies differences in the patterns of jaw movements that may be due to differences in the structures of the temporomandibular joint. Carnivores have a hinge-like temporomandibular joint that constrains lateral

movements of the jaw, whereas the jaw moves laterally in most other animals (Luschei and Goldberg, 1981; Hiiemae and Crompton, 1985). In many species, including man (Hiiemae and Crompton, 1985), chewing typically occurs on one favored (working) side. When teeth make contact with food, the speed of jaw closing is reduced, and the activity of jaw closers on the chewing side rapidly increases to generate appropriate masticatory force. Once food is crushed, the jaw shifts back medially, which causes further food grinding. Based on jaw-closing speed, the early part of jaw-closing is called the fast-closing (FC) phase, and the subsequent part, the slow-closing (SC) phase (also called the power phase). Thus, each cycle of the reduction series has three phases: jaw-opening, FC, and SC and is referred to as the three-phase cycle (Schwartz et al., 1989; Yamada and Yamamura, 1996). Such a pattern of jaw movements occurs in man (Hannam et al., 1977; Morimoto et al., 1984), monkey (Luschei and Goodwin, 1974; Larson et al., 1980) and rabbit (Morimoto et al., 1985; Schwartz et al., 1989; Yamada and Yamamura, 1996).

The first extensive study of the activity patterns in various orofacial muscles during this period was conducted in man by Møller (1966). Subsequent studies in various species confirmed and extended those findings, indicating that the basic features of the jaw, tongue and facial muscle activity during mastication are common to many animals. The digastric (major jaw opener) activity commences in the early part of the jaw-opening phase, but its activity rapidly increases during the second half of the jaw-opening phase (Schwartz et al., 1989). In some animals, such as cat, opossum and rabbit (Fig. 1), the opening phase may be in two parts (fast- and slow-opening) separated with a pause (Thexton et al., 1980; Hiiemae and Crompton, 1985).

During jaw closing, the jaw first moves laterally to the chewing side (FC

phase), and food is crushed and ground between the molars by the medially directed power stroke (SC phase). In the rabbit, which has prominent lateral jaw movements, the activity of the masseters of the opposite sides differs. The activity on the chewing side increases abruptly at the beginning of the SC, while that on the non-chewing side commences and reaches its peak somewhat earlier (Ootaki et al., 2004). Weijs and Dantuma (1981) found that such temporal differences between the sides contributes to the lateral shift of the jaw during closing.

For food to be broken down, it must first be positioned between the occlusal teeth surfaces on the chewing side; movements of the tongue and cheeks play a major role in this (Casas et al., 2003). Kinematic studies show that the tongue and hyoid have cyclic movements synchronous with jaw movements (Hiiemae, 1978; Hiiemae and Crompton, 1985; Hiiemae et al., 1996). Movements of the tongue and hyoid start before the jaw reaches the minimum gape (end of the SC phase) (Hiiemae and Crompton, 1985). At this time, the hyoid is at its most depressed and retracted position. As the jaw begins to open, the hyoid moves upward and forward, the intermediate and posterior parts of the tongue start to protract, and the tongue lengthens. Then, the directions of movements of the hyoid and tongue suddenly reverse, and the tongue shortens during the middle to late part of the jaw-opening phase (Fig. 2).

Consistent with the above findings, the tongue and/or hyoid muscles show rhythmic activities with the same rhythm as that of the jaw muscles (cat (Thexton and McGarrick, 1994), rabbit (Meng et al., 1999; Naganuma et al., 2001; Inoue et al., 2004), monkey (Yamamura et al., 2002), man (Takada et al., 1996)). Based on the period in which their main burst of activity occurs in relation to jaw movements, the tongue, hyoid and jaw muscles are divided into opening phase (OP)-active and closing phase

(CL)-active groups. The former includes the GG, geniohyoid and jaw openers, and the latter the styloglossus, sternohyoid and jaw closers (Liu et al., 1993). Fig. 3A shows examples of recordings during the reduction series in an awake rabbit. Double-peaked EMG activities (i.e., two peaks within a chewing cycle) occur in many muscles except the jaw closer, suggesting a complex movement of the tongue (and the hyoid as the tongue base). Such a complex activity pattern for the hyoid also occurs in cats (Thexton and McGarrick, 1994). A low level of tonic activity is also present in the tongue and hyoid muscles during the inter-burst period; this probably helps stabilize the resting position of these muscles.

Facial muscles such as the orbicularis oris and buccinator also are rhythmically active in man (Møller, 1966; Schieppati et al., 1989; Takada et al., 1996) and rabbit (Ootaki et al., 2004). As is the case for the tongue and hyoid muscles, double-peaked EMG activities (especially in the buccinator) and small EMG activity during the inter-burst period are frequently observed (Fig. 3B). There is a significant difference in the EMG activity in the buccinator between the chewing and non-chewing sides in rabbit associated with prominent lateral movements of the jaw (Ootaki et al., 2004). However, this was not observed in man, who have limited lateral movements of the jaw (Blanton et al., 1970; Schieppati et al., 1989).

3.3. Preswallowing series (Stage IIb or preswallow period)

This period was studied in rabbit (Morimoto et al., 1985; Schwartz et al., 1989; Yamada and Yamamura, 1996; Ootaki et al., 2004), cat and opossum (Hiiemae, 1978), monkey (Narita et al., 2002; Yamamura et al., 2002) and man (Hiiemae et al., 1996). In most cases, its onset is marked by reduced activity in jaw closers. The jaw, hyoid and tongue move in a well-coordinated manner during this period (Hiiemae, 1978; Hiiemae

et al., 1996; Narita et al., 2002; Yamamura et al., 2002). Facial muscles also show rhythmic activity with the same rhythm that of the jaw muscles, but in contrast to the reduction series, both sides are synchronized (Ootaki et al., 2004).

4. Neural mechanisms underlying coordinated activities in the cranial motoneurons during mastication

4.1. Central pattern generator for mastication

The masticatory central pattern generator (CPG) comprises groups of neurons that can produce masticatory-like movements even when isolated from other brain structures and sensory inputs. It is generally subdivided into rhythm-generating and burst-generating components (Lund, 1991; Nakamura et al., 2004). The essential structures for the masticatory rhythmogenesis were initially identified in the medial bulbar reticular formation, including nuclei reticularis paragigantocellularis and gigantocellularis (Nozaki et al., 1986). Inputs from the cerebral cortex and V afferents drive neurons within the paragigantocellularis; at this level, neurons fire tonically. These neurons monosynaptically drive neurons within the gigantocellularis that establish the masticatory rhythm. The outputs from the rhythm-generating components then drive the burst-generating components located in the caudal regions of the lateral parvocellular reticular formation where many V premotoneurons exist (see (Lund, 1991; Nakamura and Katakura, 1995) for reviews).

Studies on the neural mechanisms of masticatory rhythmogenesis have primarily focused on rhythmogenesis in the jaw (i.e., V) motoneurons. Less attention has been paid to other cranial (VII and XII) motoneurons showing rhythmic activity synchronized with jaw motoneurons. The view that masticatory CPG also regulates

activities of VII and XII cranial motoneurons is supported by anatomical evidence that some medulla neurons within or adjacent to the masticatory CPG project to both V and VII or to both V and XII motoneurons.

Spinal motoneurons participating in cyclic motor behaviors controlled by CPGs generally manifest a rhythmical alternation of excitation and inhibition (e.g., spinal respiratory (Sears, 1964; Milano et al., 1992) and locomotor (Grillner, 1981) motoneurons). However, this is not the case for motoneurons involved in masticatory movements. For example, jaw closer and opener motoneurons are alternatively depolarized during fictive mastication, but only the former undergo rhythmic hyperpolarization (cat (Nakamura and Kubo, 1978), guinea pig (Chandler and Goldberg, 1982)). Likewise, XII motoneurons do not display hyperpolarization between consecutive depolarization during fictive mastication in cats (Sahara et al., 1988). Interestingly, a similar activity pattern was reported for many respiratory-modulated cranial motoneurons (VII (Huangfu et al., 1993), XII (Withington-Wray et al., 1988; Woch and Kubin, 1995; Peever et al., 2002) and some laryngeal motoneurons (Barillot et al., 1990)). The findings suggest a similarity between the organization of the pathways that mediate the masticatory and respiratory rhythms to orofacial motoneurons. Also the lack of hyperpolarization in these motoneurons may increase the effectiveness of excitatory sensory inputs in modulating these motoneuronal activities.

4.2. Regulatory mechanisms of mastication-related cranial motoneuronal activities by the cerebral cortex

Stimulation of the lateral part of the cerebral cortex induces rhythmic jaw movements in many mammals (monkey (Huang et al., 1989; Sessle et al., 1995), cat

(Iwata et al., 1990), guinea pig: (Goldberg and Tal, 1978), rabbit (Lund et al., 1984; Liu et al., 1993), rat (Sasamoto et al., 1990)). Such rhythmic jaw movements with coordinated rhythmic movements in the tongue and facial organs as well as saliva secretion are called “fictive mastication”, and the cortical region inducing these rhythmic jaw movements is termed the “cortical masticatory area (CMA)”. At present, descending input from the CMA is considered the major source generating (activating) the masticatory CPG (Nakamura and Katakura, 1995). The importance of the CMA in the control of masticatory movements has been suggested in patients and experimental animals showing that damage to this cortical region disrupts masticatory movements (Penfield and Rasmussen, 1950; Larson et al., 1980; Enomoto et al., 1987; Freund, 1987). In addition, single neuronal recordings have revealed that many cortical neurons show altered activity in relation to mastication, and that several different mastication-related activity patterns exist (Kubota and Niki, 1971; Lund and Lamarre, 1974; Yao et al., 2002). The findings suggest that the CMA plays more roles than just generating the masticatory CPG.

The cortical regions classically considered as “CMA” include several spatially and cytoarchitectonically distinct cortical regions in many animals. For example, four cortical regions have a representation of rhythmic jaw movements in monkey: the face primary motor cortex (face MI), the face somatosensory cortex (face SI), the area immediately lateral to the face primary motor cortex (CMAp), and an area deep to the CMA at the inner surface of the frontal operculum (CMAd) (Huang et al., 1989). Similar observations are also reported for other mammals. Unlike locomotion, a kinematical pattern of cortically-induced rhythmic movements of the jaw and associated orofacial structures varies depending on the stimulus site within the cortex (Lund et al.,

1984; Huang et al., 1989; Sasamoto et al., 1990; Liu et al., 1993). These findings raise the possibility that several cortical regions are involved in the control of masticatory movements, and that each cortical region may play a different role in the production or control of mastication. Nonetheless, the role of the cerebral cortex in the control of masticatory movements was viewed as a superimposition of a repertoire of specific motor synergies principally on subcortical circuits, including the masticatory CPG (Luschei and Goldberg, 1981).

However, Sessle and colleagues presented a view that the programming of muscle activities occurring during mastication may not be reliant only on the masticatory CPG but also on corticofugal influences (Sessle et al., 1995, 1999). By studying the effect of bilateral reversible inactivation of functionally different cortical regions on masticatory movements and related muscle activities in awake monkeys, they suggested that 1) the CMap plays a significant role in the initiation and maintenance of mastication and in the regulation and coordination of muscle activities throughout the masticatory period (Narita et al., 2002), and 2) the MI plays an important role in coordinating the tongue and jaw movements that are required to ingest and transport food during the food preparatory period (i.e., preparatory series) (Yamamura et al., 2002).

Single neuronal recordings have shown that many face MI neurons have an orofacial receptive field (Sessle et al., 1999; Yao et al., 2002; Hiraba, 2004) and are active during the food preparatory period (Yao et al., 2002), suggesting that sensory-motor integration is important for shaping the output patterns from the face MI during the preparatory series. However, the source of sensory inputs to the face MI is still unresolved (mainly via face SI: cat (Hiraba, 2004); and mainly other than face SI:

monkey (Yao et al., 2002)). Also, the effect of the inactivation of the face SI on orofacial motor coordination during mastication is contradictory (causes impairments: cat (Hiraba et al., 2000); relatively ineffective: monkey (Lin et al., 1998)).

4.3. Influence of sensory afferents on the coordination of V and XII motoneurons

Masticatory movements generate various orofacial sensory inputs via the V nerve (e.g., epithelial mechanoreceptors and periodontal mechanoreceptors (Appenteng et al., 1982; Olsson et al., 1988), temporomandibular joint receptors (Lund and Matthews, 1979), jaw-closing muscle spindles (Goodwin and Luschei, 1975; Taylor et al., 1981; Masuda et al., 1997) and Golgi tendon organs (Lund and Matthews, 1979)). The importance of orofacial sensory inputs in modulating masticatory movements has been demonstrated particularly for jaw muscles; for example, studies have shown that sensory feedback from the jaw-closing muscle spindle and periodontal receptors are particularly important in adaptive modifications of the jaw-closer activities (Lavigne et al., 1987; Inoue et al., 1989; Morimoto et al., 1989).

When considering the pattern of coordination between the jaw (i.e., V) and other cranial motoneurons during mastication, the following question is pertinent: “What happens in the other cranial motoneurons when the activities of the jaw motoneurons are reflexively modulated by mastication-generated sensory inputs?” Attempts to answer this question have so far been conducted only for tongue and hyoid motoneurons.

As noted in section 2, muscles of the tongue, hyoid, as well as jaw muscles are divided into the OP-active and CL-active groups. Liu et al. (1993) tested the effects of load perturbation on the activity patterns in these muscles by inserting polyurethane-foam strips between opposing molars during fictive mastication in

anesthetized rabbits. They showed that the activities (duration and amplitude) of the CL-active group were enhanced in proportion to the increase in the hardness of the test strip, whereas those of the OP-active group were not obviously affected. By blocking the sensory nerves from the upper and lower molar teeth, Ariyasinghe et al. (2004) suggested that the enhancement of the activity of the CL active group was induced mainly by activation of the periodontal receptors. The findings suggest that the activity of the OP-active group (e.g., jaw-opener and tongue protractor) is stable during mastication, while that of the CL-active group (e.g., jaw-closer and tongue retractor) is susceptible to mastication-generated load perturbations. This view has subsequently been confirmed by studies in awake rabbits; in which EMG activities of these muscles were recorded while animals chewed test foods with different consistency (Kakizaki et al., 2002; Inoue et al., 2004; Inoue et al., 2004).

In addition to the response characteristics of rhythmic burst activities to load perturbation, similarities in the response characteristics in both the OP- and CL-active groups were also demonstrated for other types of V sensory inputs. During mastication, especially of hard food, an excitatory reflex in jaw openers (digastric short burst: DSB) and an inhibitory reflex in jaw closers (masseteric inhibitory period: MIP) are reported to be induced by strong mechanical stimulation of the periodontal receptors (Haraguchi and Yamada, 1992; Yamada and Haraguchi, 1995). Kakizaki et al. (2002) found that similar responses are also induced in the tongue muscles, i.e., genioglossus short burst (GGSB) coincides with the styloglossus inhibitory period (SGIP) in awake rabbits. They reported that GGSB-SGIP and DSB-MIP occurred simultaneously in most cases, indicating that strong mechanical stimulation of the periodontal receptors may induce excitatory reflexes in the OP-active group and inhibitory reflexes in the

CL-active group.

The jaw reflex evoked in the OP-active group by V nerve stimulation (jaw-opening reflex) is known to be modulated in a phase (i.e., opening, FC and SC phases) dependent manner during mastication (Lund et al., 1983; Haraguchi et al., 1994; Yamamura et al., 1998). Although general response characteristics to sensory inputs are similar in both OP- and the CL-active groups, considerable differences between V and XII motoneurons of the same muscle group was reported for neural mechanisms regulating the reflex response; Aebe et al. (Aebe et al., 2002) showed that the reflex evoked in tongue muscles of the OP-active group (genioglossus reflexes) by V nerve stimulation is also modulated in a phase dependent manner, but that the pattern of modulation was different from that of the jaw-opening reflex.

5. Concluding remarks

The brainstem CPG plays an essential role in the control of cranial motoneurons during masticatory movements. Both the masticatory CPG and its final motor output are modulated by direct and indirect corticofugal influences and by peripheral sensory inputs. Many questions of movement coordination among different orofacial organs during mastication remain under-investigated. It is clear that the tongue, hyoid and facial muscles are very important for the smooth completion of the entire masticatory sequence. Therefore, although masticatory movements are frequently seen as "cyclic jaw movements and associated facial and tongue movements", muscles other than those innervated by trigeminal motoneurons may play a lead role in certain aspects of masticatory movements (e.g., during food transport and the preparatory and preswallowing series). Further research at molecular, cellular, systemic and behavioral

levels is needed to determine the mechanisms of this important rhythmic behavior involving multiple orofacial muscle groups.

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Figure legends

Fig. 1

A typical masticatory sequence during bread chewing on the right side in a freely behaving rabbit. Vertical, Horizontal and Head movements, bilateral masseter (major jaw closer) and digastric (jaw opener) muscles and right side thyrohyoid (THY) muscle activities are shown in A. B shows reconstructed jaw movement trajectories in the frontal plane in each time period (a: preparatory series; b-1, b-2, b-3: reduction series; c: preswallow series). Swallow events can be determined by the conspicuous THY bursts (indicated by arrows S1 and S2). Note that two types of swallow events occur during this masticatory sequence, i.e., interposed swallow (S1) and terminal swallow (S2). PREP: preparatory series; RED: reduction series; PRES: preswallowing series; VERT and HORZ: Vertical and horizontal components of the jaw movement trajectories, respectively; MAS: masseter; DIG: digastric; R-: right side; L-: left side; FC: fast-closing phase; SC: slow-closing phase. Modified from Yamada and Yamamura (1996).

Fig. 2

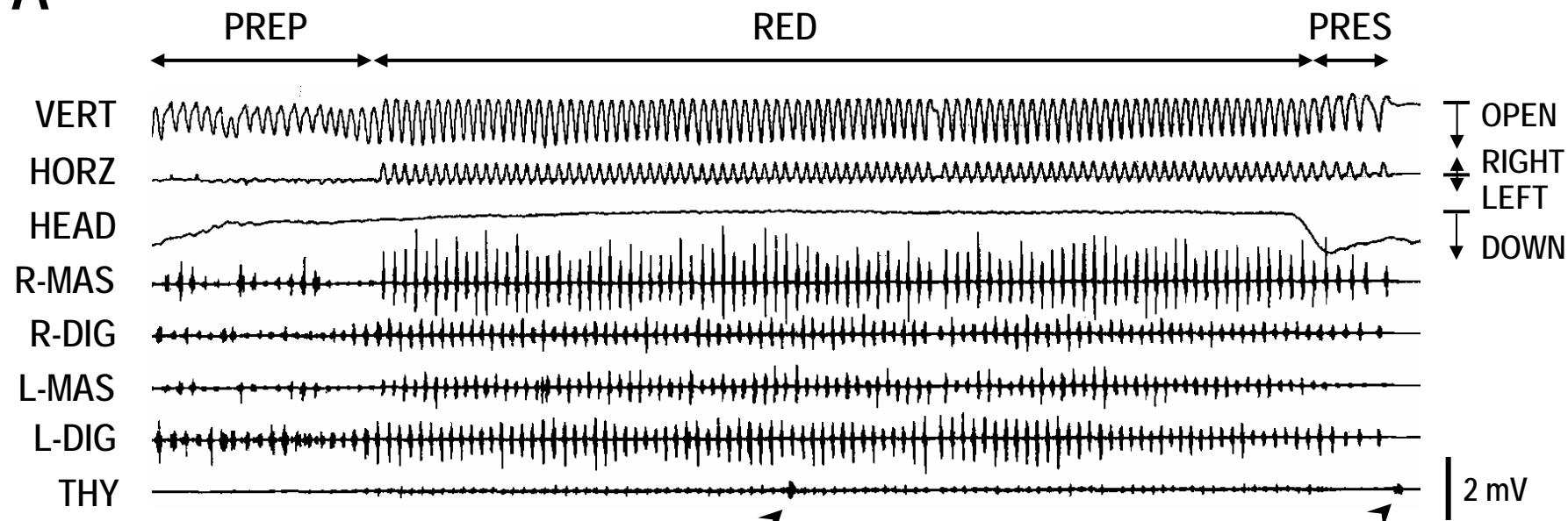
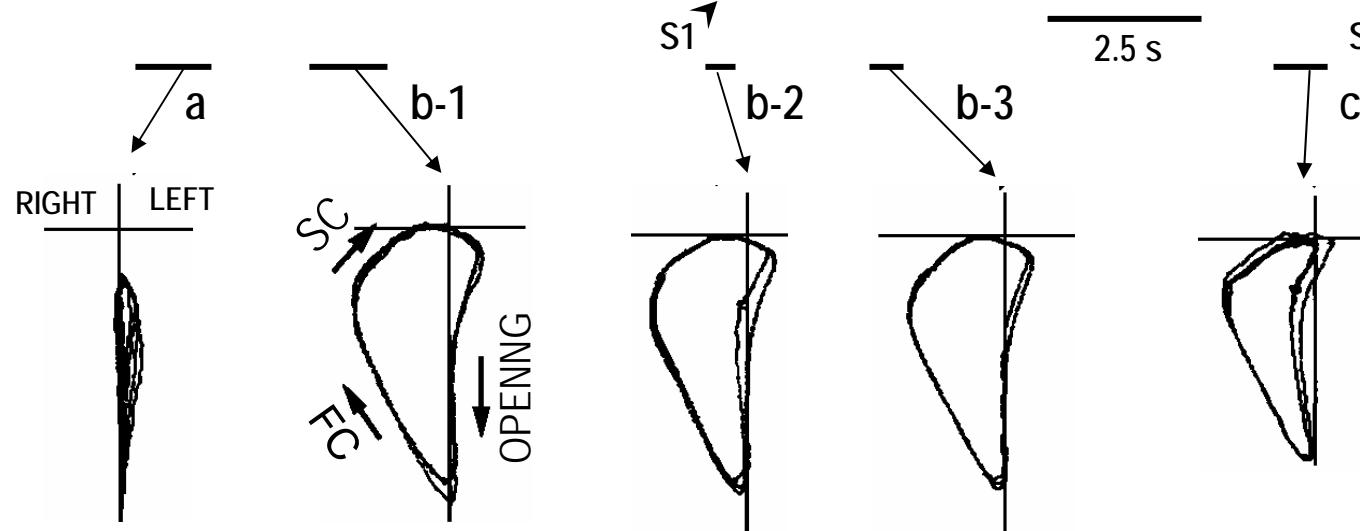
The relationship of tongue and hyoid movements to the jaw movement cycle. This type of jaw movement with two jaw-opening phases is observed in hyrax and opossum. Hyoid and tongue movements correlate with jaw movement at minimum gape when the hyoid and posterior two thirds of the tongue begin to protract and the posterior third to expand. Note that the direction of hyoid and tongue movements abruptly reverse during the middle part of jaw opening, which indicates that jaw opening is not a simple motor event dependent on the activity of the jaw opener. FC: fast-closing phase; SC:

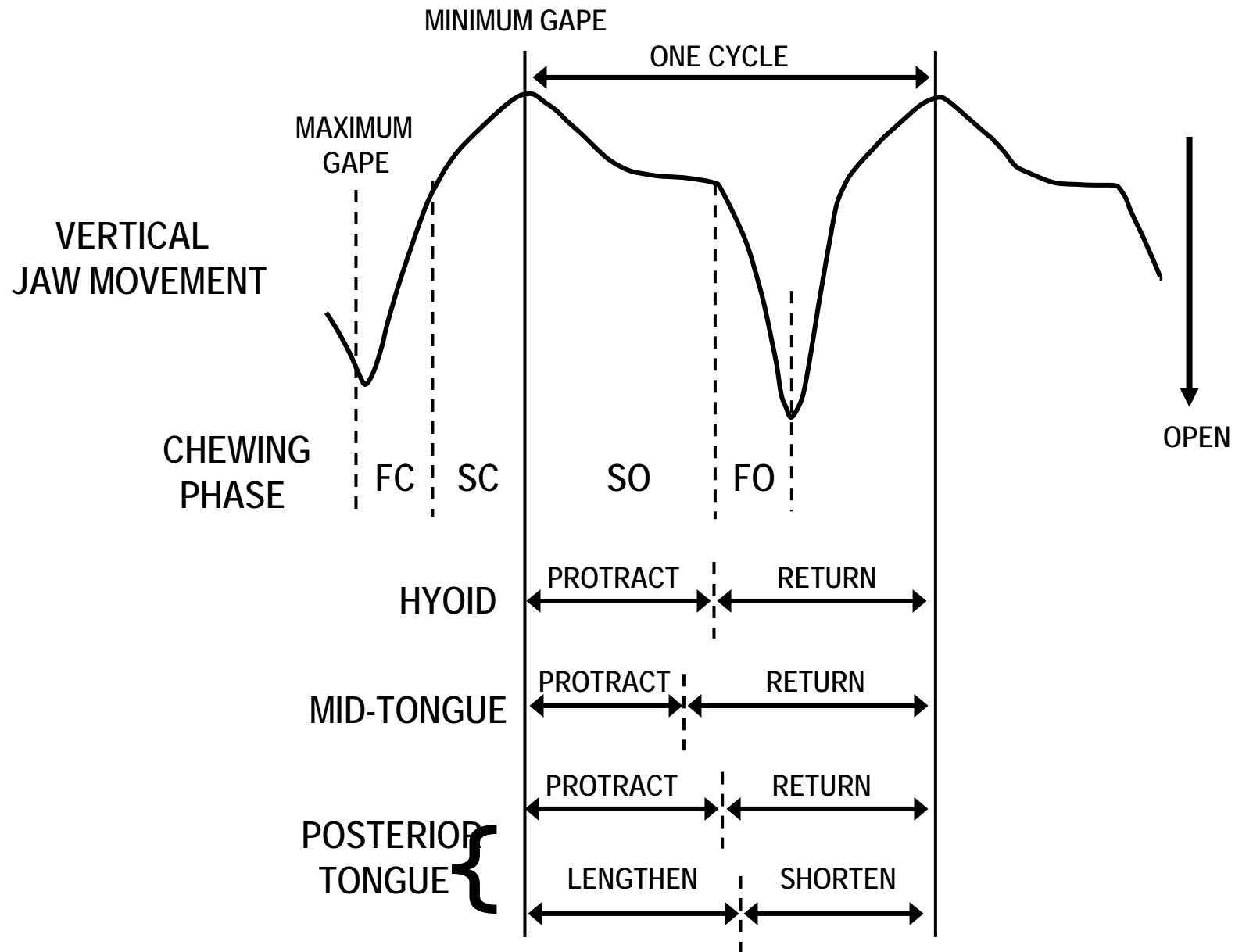
slow-closing phase; SO: slow-opening phase; FO: fast-opening phase. Modified from Hiiemae and Crompton (1985).

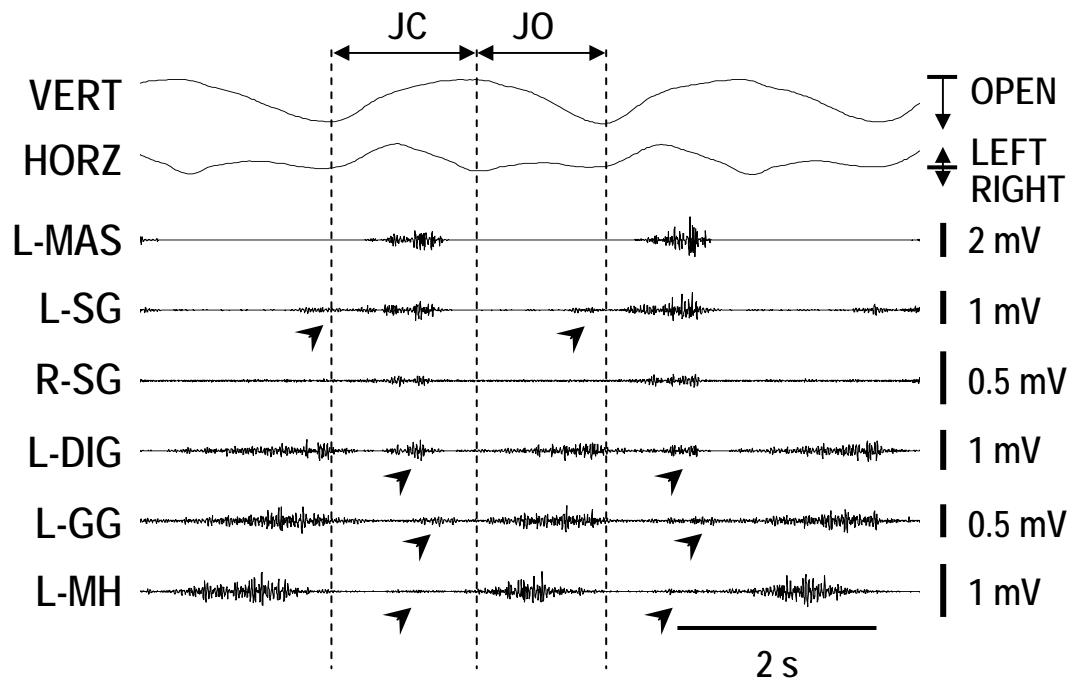
Fig. 3

Recordings of jaw movements and jaw EMG activities, and EMG activities in hyoid and tongue (A) or facial (B) muscles in a reduction series during chow pellet chewing on the left side in a freely behaving rabbit. Jaw, hyoid and tongue muscles are rhythmically active (A). The masseter and styloglossus muscles are active during the jaw-closing phase, and the digastric, mylohyoid and genioglossus muscles are active during the jaw-opening phase. Facial muscles also show a rhythmic burst; note that a prominent time difference exists in the buccinator (BUC) bursts between the sides. Note that small bursts are observed in many muscles in addition to their main burst in each chewing cycle (indicated by arrowheads).

JC: jaw-closing phase; JO: jaw-opening phase; SG: styloglossus; GG: genioglossus; MH: mylohyoid; ORB: orbicularis oris. Other abbreviations are the same as in Fig 1.

A**B**



A**B**