Neural Control of Oral Somatic Motor Function

SUZANN K. CAMPBELL, PhD

The control and regulation of mastication and other basic oral activities require integration by brain stem cranial nerve nuclei of reflex inputs and commands from other central nervous system nuclei. A current conceptual model for understanding control of rhythmic oral motor activity postulates the existence of a central pattern generator, which produces the sequence of movements common to many oral functional activities. According to this model, the output of the generator can be influenced by activity in cranial nerve afferents or modified by signals from other central nuclei. The central control model predicts that the threshold for reflex responses will change during the jaw opening and closing phases of mastication so that the effect of sensory stimulation will vary with the concurrent activity of the muscular and central nervous systems.

Key Words: Motor activity, Jaw, Mastication, Central nervous system, Movement.

Oral motor evaluation involves assessment of oral posture and movement. Therapy for patients with congenital abnormalities or nervous system damage consists of sensory stimulation to evoke movement and use of manual control to stabilize the jaw and inhibit abnormal movements. The goal of therapy is to restore, improve, or prevent deterioration of muscle tone and responsivity to stimulation and to aid the patient in attaining functional control of posture and movement. To do this most effectively and appropriately, it is very useful to know as much as possible about the normal kinesiology and neural regulation of oral motor function. The purpose of this paper is to provide the reader with information on posture and movements of the jaw and their control by the nervous system.

Although the normal resting position of the jaw is known, the static and dynamic determinants of resting muscle tone are not completely known. Similarly, the sequence of movements and muscular activity during mastication and other rhythmical jaw movements is known, but several competing models have been postulated to explain how these activities are initiated and controlled by the nervous system. Questions regarding the nature of the modification of movements under varying conditions, such as chewing hard versus soft food, are difficult to answer because cranial nerve somatic motor function is more complex than that of spinal segments. The oral, pharyngeal, and laryngeal muscles are often involved in several concurrent activities, such as respiration, phonation, and deglutition. An incredible amount of sensory information from contacts of teeth, tongue, palate, lips, and other buccal structures—with food and with each other—activates several types of receptors and is distributed within circuits of the CNS.

A large number of brain stem nuclei participate in the control of jaw movements, and each may integrate information from several ascending and descending sources. Reflexes resulting in jaw opening or closing have been extensively studied, and current work is bringing us closer to understanding the interaction of reflexes with voluntary movement. Knowledge of research on modification of the influence of reflexes on oral function may be valuable to therapists planning oral sensorimotor programs for patients.

This paper will review data and one current conceptual model concerning control of oral postures and mandibular movements. Discussion of the neural circuits (including afferent, efferent, and interpolated nuclei) subserving oral somatic motor function will be included.

Ms. Campbell is Associate Professor, Division of Physical Therapy, Department of Medical Allied Health Professions, School of Medicine Wing C, Bldg 221H, University of North Carolina at Chapel Hill, Chapel Hill, NC 27514 (USA).

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RESTING POSTURE OF THE JAW

Following reflex or voluntary movement, the jaw returns to its normal, or "rest," position. This posture is somewhat arbitrarily defined, inasmuch as the jaw is seldom held in a fixed position. The rest position of the mandible is "the postural base from which all articulatory, masticatory, and swallowing movements of the lower jaw are initiated and to which the jaw automatically (that is, reflexly) returns when such activity is terminated." In this section, the possible muscular and neural determinants of the rest position will be described.

Controversy abounds in the literature over the determinants of the rest position. These determinants may include 1) the static elastic properties of connective tissue in muscles, 2) the static elastic properties of muscle fibers, and 3) the number, size, and firing frequency of motor units, a dynamic component regulated by neural circuits. The controversy is between those who believe that the rest position of the jaw is determined purely by static properties (that is, the intrinsic elasticity of muscle, which tends to close the mouth or keep the mouth closed) and others who believe that low-frequency firing of motor units is necessary to contract the muscles to maintain this position. In support of the latter idea are the facts that, when falling asleep, a person's mouth tends to open, and that in certain neurological conditions, such as parkinsonism, the normal closed-mouth position cannot be maintained. Studies required to validate one or the other of these views do not appear to have been undertaken. Most attempts at recording from the appropriate muscles have used surface electrodes, which cannot adequately assess the low level of muscle activity that might be present.

In support of the former idea, studies of other muscles of the body indicate that the static elastic properties of muscle are at least as important as are stretch reflexes in maintaining postural set. Current information on human subjects shows that the stretch reflex provides only a small amount of compensation for a load applied to a muscle. Rather, initial compensation for an applied load is provided by static elastic properties of the muscle. Later, a small compensation is effected by the stretch reflex. Still later, effective recovery of position is attained through central reprogramming of motoneuron activity. As with the control of limb position, however, static and dynamic determinants apparently act synergistically to provide a fine degree of postural control for the jaw.

If motor unit firing is present while the mandible is in the resting position, the source of neural activity would be neurons in the motor trigeminal nucleus (cranial nerve V nucleus), which is the most rostral of the nuclei that innervate muscles deriving ontogenetically from the branchial arches. The nucleus is located in the mid-pons and contains several individuated groups of motoneurons, each of which innervates a different specific muscle. These muscles include the muscles of mastication, the tensor veli palatini, the mylohyoideus, and the anterior belly of the digastricus. The fifth motor nucleus receives corticobulbar fibers and, through interneurons, fibers from the brain stem reticular formation and other cranial nerve nuclei. Afferents from the mesencephalic trigeminal nucleus, a sensory nucleus containing cell bodies activated from muscle spindles in jaw muscles, are important because this nucleus mediates proprioceptive reflexes. Afferents from cervical and temporomandibular joint receptors and from neurons in the reticular formation and deep cerebellar nuclei activate primarily fusimotor neurons in the motor trigeminal nucleus. With different body and head positions, afferents from medullary vestibular circuits have effects on muscle tone and may exert an important influence on the firing frequency of motor units involved in postural control of the jaw.

MOVEMENTS OF THE JAW

Superimposed on a base of postural tone, the jaws participate in a wide variety of activities, including movements relating to vegetative functions, communication, and perception. In mastication, the movement itself is the primary activity and sensory input guides the action. In other movements related to exploration and discrimination, such as mouthing in infancy, the experience of sensation is the primary activity. Varying perceptions are generated by moving different receptor sheets discriminatively over objects and surfaces. This section of the paper will describe the kinesiology of basic masticatory movements and the brain stem circuits controlling mastication, deglutition, respiration, and facial expression.

Kinesiology of Mastication

Regardless of whether a person is biting, chewing, licking, suckling, or grinding, the sequence and rate of the component movements is similar. The pattern of muscle activity varies, but, in general, the basic pattern is invariant for a given individual, and the control mechanism is likely to be the same for all oral movements. Understanding the neural control of rhythmical jaw movements requires knowledge of the complex kinesiology of oral activity during basic masticatory functions. The phases of mandibular activity during rhythmic chewing have been described.
by Watt, who analyzed 1) the sounds produced in the mouth during chewing, 2) EMG activity in working muscles, 3) high-speed cinematography, and 4) pressure-transducer records derived from the force of the teeth against each other and on a chewable oral insert. Subjects chewed on gum, peanuts, biscuits, apples, and special force transducers.

The first phase of mastication is a closing phase initiated from a relatively depressed position of the mandible in which EMG activity is present in the jaw elevator muscle. Some investigators claim that a simultaneous lengthening contraction occurs in the digastricus, meaning that the jaw opening muscles elongate while continuing to contract as the jaw closes. Second is the contact phase, when the teeth begin to touch. As this happens, the velocity of mandibular closing decreases until the movement ceases. This phase, in which there are contacts between hard tissues as the teeth strike together during chewing, makes oral motor function very different from motor activity in the rest of the body.

When the movement of the mandible ceases, a "squeeze" phase occurs. The teeth are not colliding during this phase; they have achieved an equilibrium with the cusps interdigitated. Peak tooth pressure as measured by force transducers occurs during this phase of the cycle, and the masseter shows isometric activity, the so-called squeeze. The force developed in this phase of the cycle appears to be partially dependent on sensory input, because anesthesia of periodontal mechanoreceptors considerably decreases bite force. Loss of muscle spindle input has not been found to produce any significant disturbance of the rhythm or sequence of activity during chewing, but loss of joint receptor input impairs mandibular positioning. In the final phase of the chewing cycle, the jaws separate, producing a negative peak in the tooth pressure recording just prior to mandibular opening and silencing of the masseter EMG.

Neural Control of Mastication, Deglutition, and Respiration

The basic pattern of muscular activity during mastication is controlled by motoneuron firing in the motor trigeminal nucleus. Coordination of all the complex muscular activity involved in mastication, however, requires participation of other cranial nerve motor nuclei as well. Working together, several nuclei located in the brain stem must integrate the activities of mastication, deglutition, and respiration.

The tongue, for example, must aid in moving food to grinding and biting surfaces, in cleaning teeth and lips, and in bolus collection and propulsion prior to swallowing. The motor nucleus of cranial nerve XII, the hypoglossal, innervates the muscles of the tongue and receives corticobulbar fibers from the motor cortex for voluntary control of the tongue. Distinct cell groups of this nucleus innervate each of the individual tongue muscles. The hypoglossal nucleus receives afferents from the reticular formation, the sensory trigeminal nuclei, and the nucleus of the tractus solitarius for mediation of reflexes and reactions to sucking, swallowing, and chewing.

Facial muscles, especially those muscles surrounding the lips, also participate in control of food in the mouth. These muscles are activated by neurons in the motor nucleus of the intermediofacial nerve (cranial nerve VII), which receives corticobulbar innervation for voluntary control.

When food has reached the appropriate consistency, the tongue and pharyngeal muscles, as well as respiratory activity, must be coordinated to produce swallowing, a propelling of the collected bolus into the esophagus and not into the trachea. The nucleus ambiguus provides the motor fibers to the pharyngeal and laryngeal muscles and to the accessory muscles of respiration over cranial nerves IX, X, and XI. This nucleus receives corticobulbar fibers for voluntary muscle control and also collaterals from various visceral and somatic afferents important in reflex swallowing, coughing, and vomiting.

The ventrolateral nucleus of the solitary tract contains cells thought to control the rhythmic pattern of respiration. These cells drive phrenic nerve activity and receive information from bronchial stretch receptors over cranial nerve X, as well as from rostral chemoreceptor centers, the cerebellum, and the spinal cord.

Neural Control of Facial Expression

The motor nucleus of the intermediofacial nerve is located just rostral to the nucleus ambiguus in the caudal pons. Distinct cell groups innervate each of the facial muscles; a lateral cell group to the oral muscles is particularly large and distinct in man. This nucleus mediates reflex responses derived from optical afferents to the superior colliculus; acoustic reflexes relayed from the superior olive; and the innate gustofacial responses, or reflex facial expressions resulting from various taste sensations. The facial nucleus receives input from the sensory trigeminal nuclei and from the nucleus of the solitary tract, so the muscles of facial expression can be activated by a number of different sensory modalities. Direct corticobulbar fibers allow voluntary control of this nucleus in man, and, at least in cats, there are fibers from the red nucleus as well. The nucleus receives bilateral projections from the reticular formation and
either direct or indirect connections from the globus pallidus of the basal ganglia.9

In summary, a number of brain stem nuclei participate in controlling the rhythmical movements of the jaw. The cranial nerve motor nuclei are musculotopically organized collections of cell bodies that may integrate information from several cranial nerve nuclei and other ascending and descending sources. Each nucleus participates in reflex responses to external stimulation, but also receives other input from the CNS that may enhance or voluntarily override the effects of peripheral reflexes. Nuclei other than the cranial nerve nuclei, therefore, also participate as central nervous system integrative centers in the control and regulation of oral-facial behavior. Before continuing with discussion of a conceptual model of neural mechanisms producing rhythmical activity, the major jaw reflexes will be described.

REFLEXES OF THE JAW

A number of major oral reflexes have been studied by neurophysiologists. The work has used primarily reduced preparations, such as anesthetized or decerebrate cats, and, to some extent, patients with neurological deficits. Little work has been done on humans with intact systems and almost none at all on human infants. We do know, however, that reflexes in the normal animal are not, by themselves, important determinants of motor activity, but rather must interact with the ongoing transactions of the neural system. According to Thexton, "Reflex responses depend as much upon what other activity is going on in the neurons making up the reflex arc as upon the structure of the arc itself."14 That is to say, reflex responses are not fixed; even the monosynaptic stretch reflex can be altered by the state of the CNS at the time of reflex elicitation.4 During chewing, sensory stimulation inside the mouth and changing muscle length and tension would tend to hinder the activities of the mouth if reflexes operated in a stereotyped way. One of the prime problems of the child with CNS dysfunction is, of course, the inflexibility of reflex activities, which interferes with normal oral-motor function. Stereotyped reflexes are most characteristic of an inflexible and abnormal CNS.

The reflexes to be discussed produce jaw opening or jaw closing.5 The same type of stimulus, however, may elicit different responses depending on the type of pressure applied, the rate and duration of the stimulation, and the site and total area of application. The major oral reflexes include the transient, or phasic, jaw closing and opening reflexes, the tonic opening reflex, and the repeating-tongue-movement reflex.

Phasic Jaw Closing Reflex

The phasic jaw closing, or jaw jerk, reflex is a monosynaptic stretch reflex produced by a tap on the mandible.5,11 The primary afferents for the reflex travel in the mandibular division of the trigeminal nerve (cranial nerve V) and have their cell bodies inside the CNS in the mesencephalic nucleus of that nerve.9 This situation is unusual because the cell bodies of the primary afferents are, as a rule, outside the CNS. All of the supramandibular muscles (the jaw closing, or elevator, muscles) have large numbers of muscle spindles.2,11 (The inframandibular, or jaw opening, muscles in man have few muscle spindles, and a stretch reflex cannot be obtained from the digastrics.)2 The mesencephalic nucleus has connections with the trigeminal motor nucleus to the muscles of mastication, completing the stretch reflex arc to the jaw elevator muscles. Unlike the spinal reflex arcs, however, little reciprocal inhibition of the mandibular depressor muscles accompanies stretch reflex facilitation of the masseter.11

The phasic jaw closing reflex can be used to illustrate the various effects that can be elicited from the same jaw-tap stimulus. If the elevator muscles are moderately contracting when the stimulus is applied, the reflex will be enhanced.14 If, however, the jaws are clenched at the time of stimulus application, the reflex response is decreased because the concurrent stimulation of dental mechanoreceptors produces inhibition of elevator motoneurons. The jaw jerk can also be depressed by applying resistance to mandibular depression at the moment the jaw is tapped.14 Voluntary contraction of muscles in other parts of the body, such as the Jendrassik maneuver, tends to enhance the jaw jerk, and a similar mechanism undoubtedly contributes to increased tone in the oral musculature of children with CNS dysfunction.

Light-touch stimuli in the mouth also tend to produce closing responses.2 Sensory afferents from the mucous membranes of the mouth and overlying skin travel to the CNS in the maxillary and mandibular divisions of the trigeminal nerve. The mandibular division also carries joint afferents; together, these afferents subserve touch, pressure, two-point discrimination, and position sense.7 The cutaneous and joint afferents have their cell bodies in the trigeminal, or semilunar, ganglion; their central processes enter the brain stem at the level of the pons. These axons form a synapse with cells in the principal sensory trigeminal nucleus, from which axons ascend to the ventrobasal complex of the thalamus and, from there, to the sensorimotor cortex. Specific areas of the principal sensory nucleus receive information over cranial nerves V, VII, IX, and X, and the nucleus is somato-
topically organized; that is, specific clusters of cells receive input from specific, delimited cutaneous areas. The principal sensory trigeminal nucleus has reflex connections to motoneurons participating in the jaw closing reflex.9

**Phasic Jaw Opening Reflex**

Intraoral mechanoreceptor stimulation produces responses that vary with the intensity and area of application and with variations in background activity of muscles. A phasic jaw opening reflex can be produced in experimental animals by electrical stimulation of oral nerves or by applying relatively heavy intraoral pressure or nociceptive stimuli.4,11 The neural circuit producing this reflex response involves afferents from periodontal mechanoreceptors with cell bodies in the mesencephalic trigeminal nucleus.11 The central processes of these sensory neurons form synapses with the appropriate neurons in the motor trigeminal (cranial nerve V) nucleus and motor nucleus of the facial nerve (cranial nerve VII), innervating the posterior belly of the digastricus, the stylohyoideus, platysma, and levator veli palatini. Reciprocal inhibition of the masseter muscle accompanies digastricus facilitation.8,11

**Tonic Jaw Opening Reflex and Repeating-Tongue-Movement Reflex**

A second type of jaw opening response, the tonic-opening reflex, is related to swallowing.4 A spread of soft material over the anterior part of the tongue elicits a peristaltic-type series of contractions in the lingual muscles called the repeating-tongue-movement reflex, which moves the food, collected into a bolus, to the back of the pharynx to produce a reflex swallow.15,16 The effective stimulus appears to be fairly soft or well-chewed food that can spread over a large area of the tongue. At the same time, reflex inhibition of jaw elevator muscle activity occurs, which tends to depress the mandible slightly as the jaw relaxes. This depression is called the tonic opening reflex.4

The numerous tongue and pharyngeal movements that result in bolus collection and end in swallowing are a complex sequence, probably involving sensory afferents in the trigeminal (cranial nerve V), glossopharyngeal (cranial nerve IX), and vagus (cranial nerve X) nerves.7 Control of the pharyngeal and laryngeal muscles is exerted by the nucleus ambiguus through the glossopharyngeal and vagus nerves. The hypoglossal (cranial nerve XII) nucleus contains the motoneurons to the tongue muscles.17

**NEURAL CONTROL OF FUNCTIONAL ACTIVITIES**

A conceptual model for understanding control of oral motor activities must explain the role of jaw reflexes in normal oral function and describe how reflex activity is integrated into other central neural mechanisms. Hypotheses remain unconfirmed, but sophisticated electrophysiological recording techniques allowing assessment of function in behaving animals are gradually providing the needed data. This section of the paper will describe a current model that postulates the existence of a central pattern generator in the brain stem that produces automatic rhythmic activity but that can be influenced by sensory or central inputs.

At one time it was believed that rhythmic oral activity was initiated by a reflex action and continued by an alternating series of reflexes, the so-called peripheral control, or reflex chain, theory.4,18 The peripheral control theory held that food in the mouth stimulates oral receptors, which activate reflex connections in the brain stem, leading to activation of the opening (depressor) muscles. This is known as the phasic jaw opening reflex. Depression of the mandible then produces a stretch on the closing muscles. Sensory information from the stretch enters the brain stem and results in a reflex contraction of the closing muscles—the phasic jaw closing reflex. Repetition of these alternating reflexes produces the rhythmic movements resulting in mastication. One problem with the peripheral control theory is that reflexes normally occur more quickly than do chewing movements, so the timing of reflex responses does not fit with the rhythm observed. A second problem is that how the cycle gets started is unknown.

The fact that the sequence of movements in many oral motor activities remains the same, regardless of the specific activity occurring, suggests that there may be a central neural circuit that produces the basic patterned activity.4,18 This idea is incorporated in a new model that postulates the existence of a central pattern generator in the brain stem. The generator cells have an automatic rhythmic activity, which alternately facilitates the opening and the closing muscles.4,18 The central pattern generator can be influenced by voluntary commands from higher centers, or by sensory information from the oral cavity and from the muscles, to control or modify the output. This theory suggests, then, that the pattern is innate but can be modified by other sources. Thus reflexes and voluntary commands can be integrated with the centrally generated basic movement pattern. A unique output results, which is appropriate to the momentary environmental demand and the goals of
Figure. Hypothetical model for the control of rhythmical jaw movements. Generator neurons in circuits facilitating either the masseter (1) or the digastricus (2) muscles may be influenced both by descending pathways (3, 4) or reflex inputs from the periphery (5, 6, 7). Open circles represent facilitatory neurons. Inhibitory interneurons (black circles) provide reciprocal inhibition to the digastricus circuit during facilitation of the masseter and vice versa. Inhibition can also be expressed at the motoneuron level through segmental spinal circuits activated from peripheral receptors. (Diagram based on Thexton.4)

The organism. A reflex can be allowed to occur or reinforce a movement when appropriate to task demands, but it can also be overridden when its expression would disrupt the organized activity.

An example will summarize how such a system might operate. Olfactory and visual input from a tempting steak might produce a cortically initiated mouth opening, which turns on the central pattern generator in the brain stem as food enters the mouth. Automatic rhythmic chewing ensues without the need for conscious control; that is, we are not normally aware of the exact position of our jaw or tongue, nor of precisely which teeth are contacting the food. The texture, size, and consistency of the food, however, will provide continuously changing sensory inputs, tending to produce the appropriate reflexes. For instance, stimulation from hard food will tend to produce reflex jaw closing, but when the masticated food becomes soft, it will stimulate inhibition of elevator muscle activity and the repeating tongue reflex.8 These sensory inputs from cutaneous, muscle, and joint receptors must be integrated with the ongoing activity of the nervous system in order to produce a smoothly coordinated movement commensurate with environmental demands. When the sensory stimulus from food on the tongue produces reflex movement of the bolus to the back of the pharynx, reflex swallowing is initiated.4,15,16

Neurons possessing the appropriate characteristics of a central pattern generator are believed to exist in the brain stem reticular formation or the spinal trigeminal nuclei.19 The active neurons have a prolonged firing pattern and then suddenly stop firing. These neurons must have reciprocal inhibitory connections to antagonist muscle motoneurons, tending to turn off the activity of the opposing muscle unless those motoneurons are concurrently receiving strong facilitation for contraction from some other neural source. When the active neurons turn off, the opposing neurons are released from inhibition and they now fire, causing a reversal of movement. The result is an alternating activity of the rhythmically firing central neurons, producing opening and closing jaw movements.
These hypotheses regarding central control mechanisms can be formulated in experimentally verifiable terms. During jaw closure, for instance, the jaw opening muscles will be inhibited while the closing muscles are facilitated. The diagram of this circuit (Figure), based on the central control hypothesis, predicts that the threshold for reflex jaw opening will be increased during jaw closure. Indeed, the results of experiments show that, during closure, there is a high threshold to any stimulus that would normally tend to produce jaw opening.\(^4\)\(^11\) On the other hand, if the generator neurons go into a refractory period and stop firing, the neurons innervating jaw opening muscles are gradually released from inhibition during the last phase of jaw closure. One would predict that a strong stimulus tending to produce jaw opening could overpower the inhibition and facilitate the opening muscle. Again, various experiments have shown this to occur.\(^5\)

A similar central control theory has been postulated for the regulation of mammalian locomotion,\(^20\) of rhythmic tongue licking,\(^17\) and of respiration.\(^12\) Perhaps many of our most basic motor patterns are centrally controlled and generated. Therapists must become familiar with the data leading to development of these theories in order to consider the ongoing activity of the organism when sensory stimulation is applied. Although we cannot know the state of the CNS of a patient except by his overt behavior, the new concepts of motor control can aid understanding of variations in response to stimulation. Old concepts of reflex control of movement, which promote a stereotyped view of both therapy and the human organism, must be abandoned.

**SUMMARY**

This paper has reviewed the neural circuitry involved in control of basic oral activities and has presented a current theoretical model for understanding rhythmic oral motor patterns. The model proposes the existence of a central pattern generator that produces the sequence of movements common to many functional oral activities. According to this model, sensory stimulation can influence ongoing activity, but the specific effect will vary depending on the state of the muscular and central nervous systems.

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