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Mastication and Swallowing: 2. Control

Abstract: In recent years, it has become clear that the neural mechanisms controlling chewing and swallowing emanate from centres in the brainstem. However, these activities may be modulated by conscious processes and by feedback from peripheral nerves. This review relates this knowledge to clinical dentistry and, in particular, to the possible relationship between craniomandibular dysfunctions and impaired control of the masticatory system.

Clinical Relevance: Dentists should understand the neuromuscular control of the masticatory apparatus as this can be relevant to the general health of patients as well as to craniomandibular disorders involving the jaw muscles and joints.

Dent Update 2009; 36: 390–398

Control of mastication

The jaw muscles are 'skeletal' muscles of branchial arch origin and, as such, can be voluntarily controlled from the cerebral motor cortex via motor neurones arising in the trigeminal motor nucleus (Figure 1). However, although mastication is a voluntary action involving these skeletal muscles, it does not require much conscious effort. In this sense, it is very similar to breathing or walking. Like breathing, it is controlled principally by a *neural pattern generator* in the brainstem. This pattern generator sends out the appropriate signals to the various motor neurones which in turn control the muscles involved in mastication (Figure 1). This concept of chewing being driven by a centre in the brain was first

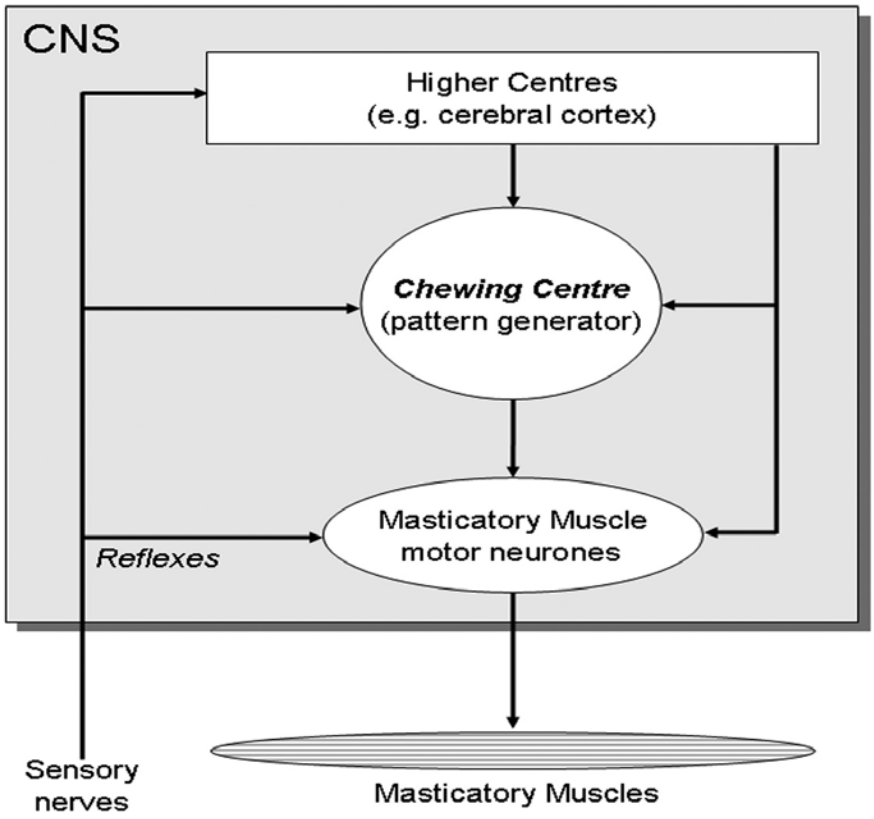

Figure 1. Mechanisms for the control of jaw movements, including during chewing (see text: cf. ref[1]). Note that, although the muscles can be controlled in various ways – including reflexly and by voluntary commands from higher centres, the main 'drive' for mastication is believed to come from a centre – a pattern generator – within the pons. Abbreviation: CNS, central nervous system.

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proposed many decades ago,[2] but the conclusive evidence for its existence in the brainstem is rather more recent.[3] It is known to lie in the pons not far from the trigeminal motor nucleus (on which it has to exert a major influence). For many years, it was suggested that it lay in the medial reticular formation at this level of the brainstem,[4] but recent studies have suggested that a more likely location is within the trigeminal main sensory nucleus[5] – a structure which one more commonly associates with the relaying of signals for the sensation of touch.

The pattern generator determines the basic sequence of muscle actions, including the order, duration and rhythm of contractions. Within this basic framework, the strengths and durations of the different phases of movement can be modified, depending on factors such as the consistency and volume of the food bolus. For example, chewing frequency is slower when eating tough foods and large boluses. This illustrates the fact that, although the basic chewing rhythm is controlled principally by the pattern generator, it can be modified by other factors (Figure 1). The chewing sequence can be over-ridden or modified by voluntary control. In the simplest scenario, signals descending from the motor cortex may work through the pattern generator to start or stop chewing or to alter the duration of the chewing cycles. In addition, there are situations where signals from higher centres may act directly on the trigeminal motor neurones to achieve a special effect, such as biting hard into food that is not being broken down by the normal chewing pattern.

The output of the chewing pattern generator is also affected by signals from peripheral sensory receptors. The importance of these for efficient chewing is obvious from the fact that chewing is so much more difficult following local anaesthesia of intra-oral structures.[6] Indeed, as shown in Figure 1, afferent (sensory) signals may alter chewing in a number of ways:

- By providing sensory information to the conscious parts of the brain regarding the physical state of the food being chewed;
- By acting on the pattern generator to modulate its activity;
- By directly affecting the activity of the motor neurones involved in mastication – by eliciting reflexes (see below).

Reflexes and mastication

Prior to the widespread acceptance that mastication is controlled by a pattern generator within the brain, most theories of masticatory control suggested that the alternating contractions of jaw opening and closing muscles were produced by the linking together of a series of reflexes.[7,8] Even though this is no longer believed, it is undoubtedly true that reflexes are superimposed on the basic chewing pattern – usually in a fashion which can be envisaged as helpful to the masticatory process. These reflexes occur in the muscles of the tongue and, arguably more importantly, in the jaw muscles. The possible roles of these reflexes in mastication are summarized below.

Tongue reflexes

Although there are a number of different tongue reflexes,[9,10] one can think of the majority falling into two main categories – those which protrude the tongue and those which retract the tongue. In general, the former are produced mainly by stimuli at the very back of the mouth or in the pharynx (ie by stimulation of glossopharyngeal or vagus nerves), while the latter are evoked principally from the main body of the mouth (notably by stimulation of lingual branches of the trigeminal nerve).[9,10] In other words, the reflexes predominantly involve the tongue being moved away from the stimulus. Thus, in simple terms, it is probably true that, with the exception of some palatal stimuli, most stimuli which occur during mastication will have an excitatory influence on tongue retractor muscles and/or an inhibitory one on the activity of tongue protruders. Conceivably, such an action might assist in the process of mastication – partly by providing space for the food bolus and partly by minimizing the likelihood of accidental biting of the tongue.

Jaw reflexes

In man and other primates, jaw reflexes occur principally, but not exclusively, in the jaw elevator muscles (masseter, temporalis and medial pterygoid). This is in contrast to other mammals in which there are also powerful reflexes in the jaw depressor muscles (digastric, mylohyoid and geniohyoid). In the context of mastication, the most important of these reflexes in man are those produced by stretching the jaw elevator muscles (the *jaw jerk reflex*) or by the presence of stimuli in or around the mouth.

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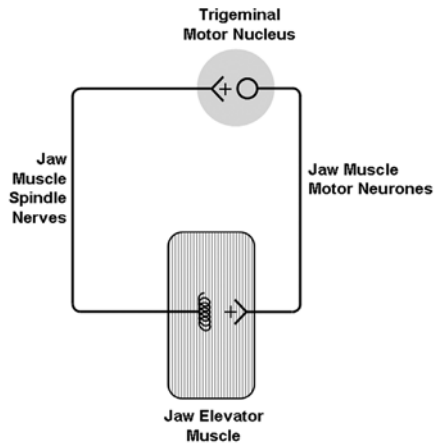

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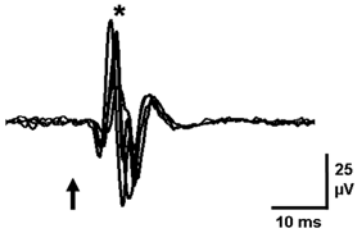

Figure 2. The *jaw jerk reflex* **(a)** schematic representation of the pathway involving just one synapse – in the trigeminal motor nucleus; **(b)** electromyographic (EMG) representation of a typical jaw jerk response in the human masseter muscle – in order to produce this response, the subject received a firm downward blow on the chin at the time indicated by the arrow – note the massive increase in EMG activity (*) which occurred approximately 5 ms later. (EMG courtesy of Dr A G Mason.)

The jaw jerk

The *jaw jerk reflex*, like the analogous *knee jerk*, may be classified as a *stretch reflex*. Such reflexes are amongst the simplest in the human body in that they are mediated by monosynaptic pathways involving just two neurones (Figure 2a). The reflex can be demonstrated by applying a downwards tap on the chin; this stretches the spindles in the jaw elevator muscles which, in turn, produce a reflex activation

of the muscles via their motor neurones. The response can be observed on an electromyogram (Figure 2b). When evoked in this fashion, the jaw jerk can be used clinically to test the health of the trigeminal motor system.[11]

Obviously, the jaw jerk is rarely, if ever, evoked by a downward blow to the chin during normal function. However, it is probably present continuously to a greater or lesser extent during chewing, as the lengths of the elevator muscles change as the jaw moves. This may help in the fine control of jaw movements to take account of varying circumstances, eg changes in the consistencies of food as it is broken up during mastication.[12] Thus, when the food is still at its most solid, the jaw elevator muscles and their spindles will be more stretched during the closing phase of a chewing cycle and will therefore produce a greater excitatory influence on the motor neurones; this in turn will assist in the generation of greater forces in an effort to break through the food. In this respect, it is helpful that the jaw jerk reflex is strongest during the closing phase of chewing [13,14] and when there is a resistance to jaw closing.[14]

Although not directly relevant to mastication, it is of interest from a clinical point of view that some research workers believe that the jaw jerk reflex (or at least a longer-lasting equivalent) may also be involved in the maintenance of jaw posture (the so-called *mandibular rest position*). For many years, there has been a dispute as to whether normal jaw posture is maintained actively by a low level of contraction in jaw elevator muscles,[15] or by passive tension in these muscles and other tissues around the jaws.[16,17] Those who argued in favour of an active mechanism suggested that the muscle activity might be generated by a stretch reflex initiated by gravitational pull on the mandible.[15] This dispute is still unresolved, although there is now a body of evidence to suggest that, even if there is a tiny amount of activity in the elevator muscles when the jaw is in its 'resting' posture, this activity does not contribute significantly to the maintenance of that posture.[18]

Jaw reflexes evoked by stimuli in and around the mouth

When mechanical or noxious stimuli are applied in or around the human mouth, the principal resulting reflexes involve inhibition of activity in jaw elevator muscles. These are sometimes said to be the human equivalent of the *jaw opening reflexes* which are seen in sub-primates and which involve activation of the jaw depressor muscles. On an electromyogram, the human reflexes usually appear as one or two periods during which any activity in jaw elevator muscles is depressed (Figure 3). Although the anatomy of the pathways for these reflexes has not been determined precisely, it is usually assumed that the reflexes are polysynaptic, having three or more synapses.[4] The importance of these inhibitory reflexes, which involve at least a cessation of jaw closing and perhaps actual jaw opening[19] is probably two-fold:

- They help to prevent overloading during chewing, of intra-oral tissues such as the teeth, and extra-oral tissues such as the muscles themselves;
- They reduce the likelihood of injury from dangerous (eg sharp) objects within food.

From a clinical standpoint, it is interesting that some of these inhibitory reflexes may be weaker[20] or absent[21] in patients suffering from craniomandibular dysfunction (CMD). It is possible that some of the pain suffered by these patients may arise from overuse of the jaw elevator muscles in the absence of this physiological check on their activity. However, given that these reflexes are also suppressed by pain and anxiety,[22] and that CMD patients often show these symptoms, it could be that the absence of the reflexes is a result rather than a cause of the clinical condition. Indeed, it is worth considering the possibility that the symptoms of the condition and the suppression of the reflexes may sustain each other (Figure 4). If this is the case, it might explain why symptomatic relief is sometimes successful in treating CMD.

Rather confusingly, it is now clear that some of the stimuli that produce these inhibitory reflexes can also produce excitatory responses in the jaw elevator muscles.[23] It has been suggested that, like the jaw jerk, these may constitute a feedback mechanism which is used during mastication to allow for different consistencies of food.[24] What is unclear is the question of under what circumstances the inhibitory or the excitatory influence predominates. One simple explanation would be that the excitatory influence dominates when the stimulus is gentle, whereas the inhibitory influence predominates when the stimulus is stronger[25] or even noxious. This is an attractive hypothesis in that boosting jaw muscle activity could be helpful during the jaw closing phase of chewing, whereas a cessation of such activity could be helpful when intra-oral tissues are at risk of damage. However, most experimental evidence does not support this hypothesis. Rather, it suggests that both types of response can be evoked by both weak and strong stimuli and that the inhibitory response is generally predominant.[4] It is possible that other factors, such as the phase of chewing (opening, closing, occlusal) or the precise

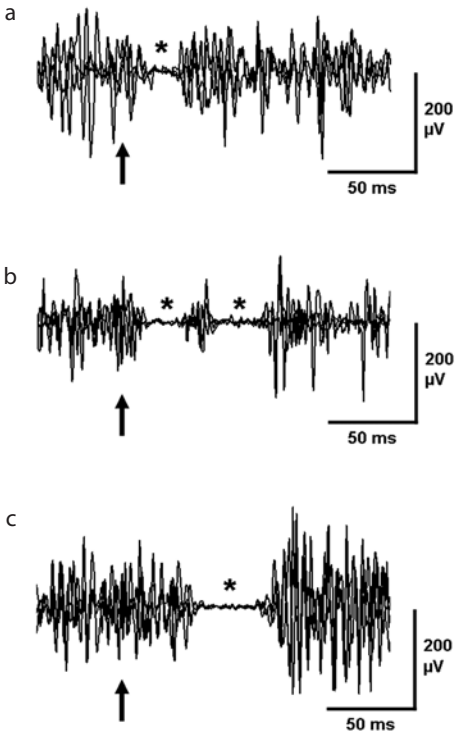

Figure 3. Electromyographic (EMG) recordings of activity produced in a human masseter muscle by biting on to a rubber impression and reflex inhibitions of that activity produced by stimuli in and around the mouth. The timings of the stimuli are indicated by the arrows; these were: **(a)** a gentle push on an upper incisor tooth; **(b)** electrical stimulation of oral mucosa; **(c)** electrical stimulation of the upper lip. Note that in every case there was one or more reflex reduction in masseter activity (*), although the pattern and timings of these reflexes differed from one stimulus to another. (EMGs courtesy of Dr A G Mason.)

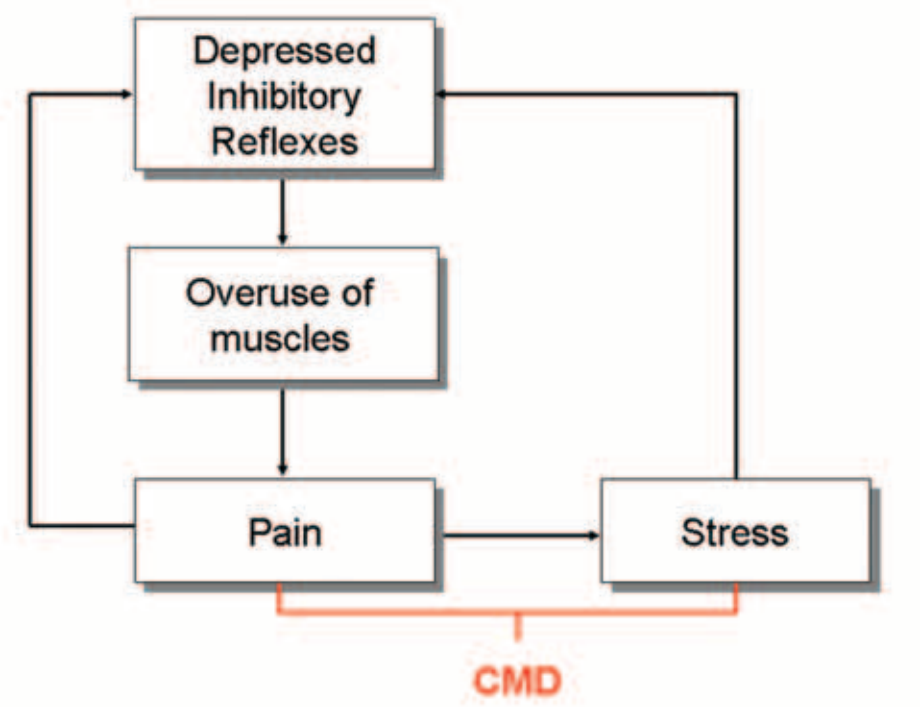

Figure 4. Hypothetical relationship between factors which suppress inhibitory jaw reflexes and the symptoms of craniomandibular dysfunction (CMD). It has been established that pain and anxiety – both common symptoms of CMD – can reduce inhibitory reflexes in jaw elevator muscles.[22] This in turn may lead to increased use of the muscles which may re-enforce the pain felt from them (see text).

location of stimuli are the ones which really matter.[26] This is an area that requires further investigation.

Jaw unloading reflex

There is one other jaw reflex which ought to be mentioned, even though its principal role is thought to be during the static biting, rather than chewing of food, namely the *jaw unloading reflex*. This reflex occurs when a hard object, which is being bitten, breaks suddenly, thus 'unloading' the jaw elevator muscles of the resistance against which they were working. The response involves a cessation of activity in jaw elevator muscles together with an activation of jaw depressor muscles.[27] It has often been suggested that this action may help prevent the teeth clashing into and potentially damaging each other. However, there is now evidence that, even in the absence of reflex actions, the physical properties of the jaw elevator muscles – notably their limited velocity of contraction following sudden unloading – may be sufficient to prevent tooth contact.[28] The exact mechanisms for the jaw unloading reflex are not known but seem to depend in part on the fact that, when we bite into something we know is brittle, we prepare our jaw depressor muscles for action as well as using our powerful elevator muscles to perform the bite.[29] Thus the depressor muscles are effectively 'primed' for the reflex action when it is triggered. (One could compare the jaw unloading reflex to what happens in the forearm during tooth extraction: when the buccal plate 'gives', control of the forceps is maintained – possibly through an unloading reflex involving antagonist muscles in the arm.)

Horizontal jaw reflexes

In addition to the jaw reflexes discussed above, which affect vertical movements of the jaws, there are believed to be horizontal jaw reflexes which involve lateral, protrusive and possibly retrusive movements of the jaw in response to stimulation of intra-oral mechanoreceptors. The evidence for the existence of these reflexes is not conclusive but, assuming they do exist, they may play a role in adjusting the final closure of the jaws from the moment of first tooth contact until the intercuspal position is reached.[9] Such mechanisms could be important in modifying jaw movements in the case of premature or eccentric contacts.

Swallowing

As we described in the companion paper,[30] chewing and swallowing are closely related. There are also similarities in the ways in which these integrated neuromuscular activities are controlled – notably in that both are driven principally by a *central pattern generator* within the brainstem. We have already discussed the pattern generator for mastication and the fact that it controls the order, duration and rhythm of the muscular actions associated with chewing. The pattern generator for swallowing can be regarded as fulfilling a similar function, albeit that the muscular actions which it controls are sequential rather than rhythmic. Of course, these actions not only have to propel the bolus towards the stomach, but also have to protect the lower respiratory passages.

A great deal of research in recent years has been directed towards understanding this 'swallowing centre' in the brainstem.[31] From these studies, it is now clear that:

- The Swallowing Centre is located in the medulla and consists of two parts (or four if one considers right and left) (Figure 5).
- The first part of the Swallowing Centre is located dorsally in the medulla, largely or wholly within the Nucleus of the Solitary Tract. This part is responsible for receiving the signals which trigger the swallowing process (see below) and for generating the patterns of neural activity required to achieve the appropriate contractions and relaxations of the muscles involved in swallowing.
- The second part of the Swallowing Centre is located more ventrally in the medulla. This ventral centre is responsible for receiving signals from the dorsal centre and relaying these to the appropriate motor neurones (which are located in the motor nuclei of cranial nerves V, VII, IX–XII and the ventral horn of the first three cervical segments (CI–III) of the spinal cord).

In simple terms, the pattern of

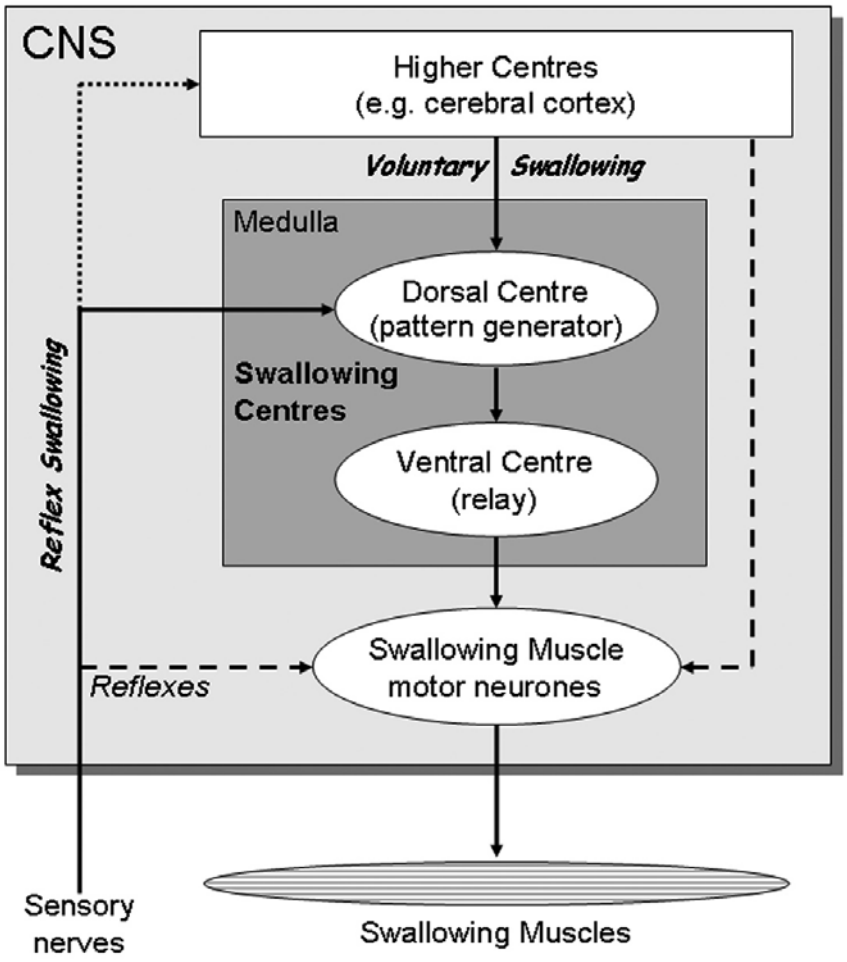

Figure 5. Diagram summarizing the control of swallowing. The pattern of muscle activity required in swallowing is set by a pattern generator in the dorsal medulla which, via a relay in the ventral medulla, controls the appropriate motor neurones (or in the case of the lower oesophagus, parasympathetic and sympathetic neurones). The pattern generator can be triggered into action by signals arising from sensory nerves (*reflex swallowing*) or from higher centres in the brain (*voluntary swallowing*) – these are indicated by solid lines. In addition, the motor neurones are subject to other influences, eg directly from sensory nerves or higher centres (broken lines) or from other pattern generators (eg for coughing). Finally, sensory signals reaching higher centres (dotted line) can influence the decision to trigger a voluntary swallow. Abbreviation: CNS, central nervous system.

activity generated by the Swallowing Centre acts on the appropriate efferent neurones to ensure that:

- The muscles ahead of the bolus become or remain relaxed (a graphic example of this would be the oesophageal sphincters); and
- The muscles around and behind the bolus contract to move it on its way. In most cases, the muscles are skeletal and innervated by motor neurones. However, in the lower oesophagus there is smooth muscle which is innervated by extrinsic parasympathetic (vagal) and sympathetic nerves as well as by intrinsic nerves in the oesophageal wall;[32,33] most accounts emphasize the roles of the parasympathetic and intrinsic nerves in controlling swallowing movements in the lower oesophagus.[32-34] In fact, it seems that the swallowing-related inhibitory influences on neurones that produce contraction or an excitatory influence on neurones that produce relaxation, occur even in respect of muscles which are usually relaxed anyway (eg those along the length of the oesophagus). In any case, these mechanisms ensure that the part of the G-I tract into which the bolus is moving will provide as little resistance as possible to the movement of the bolus.

Initiation of swallowing

Swallowing has traditionally been divided into several phases.[30,34] The first of these – the oral or oropharyngeal phase – is often described as 'voluntary', while the later – pharyngeal and oesophageal – phases are 'involuntary'. However, the vast majority of swallows occur involuntarily (genuinely voluntary swallows are difficult to achieve and are rather unnatural). Nevertheless, the term 'voluntary swallowing' persists to indicate one of the two ways in which a swallow can be initiated, namely from higher centres in the brain (Figure 5). The most obvious source of such a central drive for swallowing is from the cerebral cortex. However, there is some evidence that subcortical areas (eg the internal capsule, the hypothalamus and the mesencephalic reticular formation) can also trigger, or at least modify, swallowing.[31]

Swallowing can also be triggered by activity in sensory nerves from the oro-pharyngeal region – this is sometimes referred to as 'reflex swallowing' (Figure 5). Mechanoreceptive and chemoreceptive neurones at the back of the mouth, in the pharynx or around the epiglottis, can all trigger swallowing. These neurones belong to cranial nerves V, IX and X. Of these, it seems that the superior laryngeal branch of the vagus (Xth) nerve provides the most powerful influence – activation of it alone can trigger a swallow whereas activation of other nerves will lead to swallowing only if there is another facilitatory influence (from other peripheral nerves or from within the CNS). Indeed, the fact that food in areas innervated by the Vth and IXth nerves does not inevitably lead to swallowing is illustrated by the fact that triturated food collects on the back of the tongue during chewing and may not be displaced until the final expulsion of the main bolus from the mouth.[30]

One matter of clinical interest is the question of which stimuli at the back of the mouth produce swallowing and which produce gagging. It is well known that excess impression material contacting the posterior palate tends to cause gagging, whereas accumulation of water (from an air

rotor cooling spray) in the same region of the mouth in a reclining patient evokes a desire to swallow (although this is difficult when the jaws are wide open!). This difference could be attributed to differences in the sensory activity produced by the different stimuli, but it could also be due to factors within the brain. That central factors can affect whether we swallow or gag may be illustrated by the potential embarrassment caused by trying to swallow food which we dislike (but may feel a need to consume in certain social circumstances). In the worst scenario, we tend to gag on such food when it gets to the back of the mouth – yet food of similar consistency may be swallowed easily if we like it.

At one time it was thought that swallowing was triggered simply by the food particles having become small enough as a result of chewing. However, swallowing is not simply a matter of particle size; the physical consistency of the food is also important, eg whether it is adequately lubricated. While it is necessary to grind crunchy biscuits into small particles before they can be swallowed, one can easily swallow quite large pieces of pasta or soft fruit. Thus it seems that food particles may be swallowed when they are no longer individually detectable – and can be swallowed comfortably.[35] It has also been suggested that swallowing is initiated when food particles are sufficiently cohesive to pass through the pharynx without risk of aspiration into the airway.[36]

Feedback from sensory receptors can also modify the pattern of swallowing to make it appropriate to the nature of what is being swallowed. There is evidence that swallowing – or at least the oesophageal phase of swallowing – is slower but more powerful, the more feedback that is being received.[30] This mechanism will be helpful in moving larger boluses – these will generate more feedback and will require to be moved by a more powerful muscle contraction.

Summary

Both chewing and swallowing are co-ordinated by networks of neurons (central pattern generators) in the brainstem. The central pattern generators determine the order of muscle actions (both contractions and relaxations). The strength and duration of these actions are regulated by inputs from peripheral receptors in response to stimuli, such as the consistency and volume of the food bolus.

The muscles of the face, jaw, tongue and pharynx are also subject to reflex controls. While these reflexes can occur in isolation (eg jaw jerk reflex), they tend to be incorporated in the feeding sequence, eg to ensure that, in chewing, tongue movements are co-ordinated with jaw movements. Some reflexes are protective, eg helping to prevent overload of the masticatory apparatus during biting, or preventing food from entering the larynx during the pharyngeal phase of swallowing.

Acknowledgement

Figures 1 and 2a are based on illustrations which we have published previously (reference 4) and are reproduced with permission of S Karger, Medical and Scientific Publishers.

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