AN ELECTROMYOGRAPHIC ANALYSIS OF REFLEX DEGLUTITION

ROBERT W. DOTY AND JAMES F. BOSMA

Departments of Physiology and Pediatrics, College of Medicine, University of Utah,
Salt Lake City 1, Utah

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DEGLUTITION is a reflex coordination readily accessible and conveniently exact, yet far surpassing the integrative qualities of simpler reflex action. In a manner yet unknown, motoneurons scattered from C3 to the mesencephalon are reproducibly controlled in an intricate pattern of excitation and inhibition specific to this synergy. This paper presents an electromyographic definition of this performance and in so doing more closely specifies the necessary characteristics of its coordinative mechanism.

METHOD

Eleven dogs, ten cats, and seven monkeys under urethane or ether anesthesia were used in these experiments. For the study of the unanesthetized swallowing center some animals were prepared by severing the neuraxis immediately caudal to C1. The cord was procainized to cessation of respiration prior to cutting and cotton pledgets soaked in 2 per cent procaine HCl were inserted between the cut edges of the cord. Muscles and skin were then procainized and closed.

Swallowing was elicited by tactile stimulation of the pharynx with a cotton swab or by electrical stimulation of the central portion of the severed superior laryngeal nerve (SL). The nerve, usually contralateral to the recorded muscles, was tied into sleeve electrodes and stimulated with 10 μsec. square wave pulses, 30/sec., 2-5 V. Both rhesus and cynomolgous monkeys proved almost equal to the dog in the ease with which deglutition could be elicited by SL stimulation and were thus more readily studied than the cat or rabbit (1). The respiratory effects in the monkey were likewise similar to those in the dog.

Two electrodes of 32- or 34-gauge enamelled copper wire with insulation removed for 1-3 mm. were sewn and tied about 1 cm. apart in each muscle to be analyzed. The wires were taped together at their entrance into the muscles to reduce motion artifact. Though most electrodes were placed after surgical exposure of the muscles, all were rechecked for anatomical position at necropsy. Initially a 4- or 6-channel Offner cryostograph operated by Offner type 140-A AC amplifiers was used to record the EMG, and two channels of DC amplification recorded pressure variations from a condom rubber balloon in the pharynx and open catheter in the trachea. The results so obtained were subsequently confirmed and extended by photographing the EMG from a dual beam cathode-ray oscilloscope with a Grass 35-mm. kymograph camera operated at speeds of 10-100 cm./sec. In these experiments potentials from the two muscle electrodes were amplified in a "push-pull" arrangement through Grass P-4 pre-amplifiers and Dumont 304-H oscilloscopes. Filters were set to obtain a linear response between 5 to 500 cps. Later arrangements permitted monitoring

1 Certain phases of this work were initiated by one of us (R. D.) while enjoying a Postdoctoral U. S. Public Health Fellowship in the laboratories of Dr. Warren S. McCulloch, then at Illinois Neuropsychiatric Institute, University of Illinois. The work was continued at the University of Utah supported by the University Research Fund and by grants from the National Foundation for Infantile Paralysis.

2 Throughout the paper, use of the word "swallowing" or "deglutition" refers only to the bucco-pharyngeal stage of this synergy.
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EMG and pressure variations from pharynx and respiration on an 8-channel Grass electroencephalograph with simultaneous dual beam oscilloscope records for detailed analysis. The necessity for such oscilloscopic control must be emphasized, for there were many instances in which it was impossible to say whether the ink-writer record was spurious or genuine and CRO tracings proved definitive. Occasionally low voltage, distorted potentials (less than 50 μV.) were recorded in inactive muscles during action of those immediately adjacent, but with the CRO such artifact was readily differentiated by its rounded wave form from the spike potentials of intrinsic activity.

In most instances the bipolar technique employed provided highly selective recording. Mylohyoideus leads, for instance, were isopotential during intense action of the anatomically contiguous geniohyoideus, and vice-versa. Likewise, anterior tongue electrodes were silent during swallowing while prominent activity was registered from posterior tongue electrodes. During licking, vigorous activity was recorded from both electrode pairs. Absence of participation in swallowing was considered conclusive only if leads from the muscle in question registered activity while participating in another synergy. Leads from different parts of the same muscle or from the corresponding contralateral muscles demonstrated electromyographic activity of essentially identical time course.

OBSERVATIONS

1. Muscle coordination in deglutition

   a. General comments. Records were obtained from 22 muscles likely to participate in deglutition, most of which are shown in Figs. 1, 2 and 3 and diagrammed in Fig. 4. Swallowing activity was not seen in the masseter, temporalis, sternohyoideus, sternothyroideus or anterior intrinsic lingual muscles in any of the three species studied nor in the digastricus of cat or dog.

   The general pattern of coordination is diagrammed in Fig. 5, which summarizes observations of swallowing in the dog. The degree of activity indicated is an attempted visual integration of the fluctuation of the EMG per CRO observation. The inhibition shown is, of course, detected only when background activity is present. The background activity represented is indicative of that commonly found in these muscles during the stimulation necessary to induce swallowing; this is highly variable and often includes associated respiratory action.

   For clarity of presentation, the pattern of muscular participation in deglutition has been subdivided into three portions as follows.

   b. Leading complex. Swallowing is initiated by abrupt onset of activity in particular components of the intrinsic and supporting musculature of the rostral pharynx. These muscles of the leading complex in all three species include the superior constrictor, palatopharyngeus, palatoglossus, posterior intrinsic muscles of the tongue, styloglossus, stylohyoideus, geniohyoideus, and mylohyoideus. Activity appears simultaneously in the posterior tongue, geniohyoideus, stylohyoideus, and mylohyoideus, but the latter frequently leads by 30–40 msec. Activity in the posterior tongue usually ends 50–100 msec. earlier than in these others.

   In the monkey, though the palatoglossus and palatopharyngeus fired with the leading complex, their maximal activity is relatively delayed and they usually continue in action for 80 msec. after other lead muscles are silent. Palatopharyngeus in cat and dog typically follows the leading com-
FIG. 1

FIG. 2.

FIGS. 1, 2, 3. Musculature in region of pharynx, dog. Figure 1 is a slightly paramedian sagittal section. Figure 2, dissection from sagittal plane illustrating musculature of pharynx and larynx. Hyoglossus muscle retracted to show styloglossus. Portions of palate and thyroid cartilage excised. (See facing page for Figure 3)
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plex by approximately 40 msec. in initiation and termination of activity. Figure 6 is atypical in this regard, but properly illustrates the usual finding that maximal palatopharyngeus activity is attained well after activity in the geniohyoideus is fully developed.

c. Constrictor musculature. The pharyngeal constrictors fire in overlapping sequence (see Fig. 12). The activity in the superior constrictor is very similar to that in the anatomically related palatopharyngeus and is included in the lead group. The middle constrictor is usually inhibited during the first third of the leading complex action, then undergoes a gradual increment in activity to a maximum which is briefly sustained, followed by a gradual subsidence (Fig. 7). The inferior constrictor is inhibited during almost the entire course of lead muscle activity and its peak of action usually does not begin until after their cessation (Fig. 8). The inferior constrictor action tends to be temporally more dispersed than that of the middle constrictor and tapers off even more gradually.

d. Hyoid-laryngeal musculature. Unlike the pharyngeal constrictors and the muscles of the leading complex, those in the area of the larynx showed

Figure 3, a further dissection, illustrating musculature suspending hyoid and larynx. Palate, tongue, and portions of hyoid bone and larynx excised.
Fig. 4. Outline of neural system concerned in deglutition. Additional functions, overlapping in their afferent and efferent channels, are represented as having possible interaction with swallowing. The muscle innervation is conventional save for inclusion of retrofacial nucleus as per Szentágothai (10). Muscles shown in parentheses failed to participate in deglutition or did so to a negligible degree.

considerable species variation in the timing of their participation. The thyrohyoideus is the more constant, its initial activity following the onset in lead muscles by 45–100 msec. (Fig. 9) with inhibition frequently manifest during this interval. Action in the thyrohyoideus terminates very shortly after that of the lead group.

The thyroarytenoideus muscle, within the vocal cord, fires earlier in deglutition in the monkey, following the leading complex by only 30–80 msec. In dog and cat activity in the thyroarytenoideus usually does not begin until 150–200 msec. after activation of the leading complex; inhibition is present in this interval. In the three species studied, the action of the thyroarytenoideus terminates with or shortly after that in the lead muscles. The interarytenoideus was observed electromyographically only in the monkey, in which it was seen to fire with thyroarytenoideus.

Action in the cricothyroideus is very different in timing in each of the species, though its position in the sequence of swallowing activity is roughly comparable. In the dog inhibition is the most prominent feature, being complete for the first half of lead muscle action and moderate for the latter half (Fig. 10). An intense, brief burst of activity of 50–100 msec. duration may occur, especially when urethane anesthesia is used, but frequently inhibition
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FIG. 5. Schematic summary of electromyographic activity in deglutition for unanesthetized dog medulla. Height of line for each muscle indicates intensity of action observed, ranging from complete silence to maximum occurring in deglutition. In certain muscles, firing more intense than here represented was observed in other synergies. Action of diaphragm is that seen in eupnea. Contours of rise and fall of activity are not considered accurate. See text.

is the only sign of its inclusion in the performance of deglutition. In the cat action of the cricothyroideus follows much the same time course as the thyrohyoideus. The inhibition is present, though not as prominent as in the dog, during the period between onset in lead muscles and the cricothyroideus action. Its activity ends with that in the lead group and there is no late burst of action. Its activity in respiration is considerably greater than in deglutition.

e. Musculature unique to monkey. While the digastricus of the cat or dog was found to be silent during deglutition, the anterior and posterior digastricus of the monkey did occasionally participate. At best, however, their action is minimal compared to that seen during other synergies such as chewing. When active in deglutition, the anterior digastricus begins firing concurrently with the mylohyoideus so that it too must be considered as an-
FIG. 6. Record from etherized cat (30 May 1953). SL stimulation at 5/sec. marked by lettered arrows. Record is continuous. Activity in geniohyoideus following pulse b occurred during a licking movement, while activity following pulse e is a swallow. Small-amplitude elementary reflexes are clearly seen to follow approximately 10 msec. after pulses h and i, and a silent period of some 30 msec. follows pulses, a, b, c, e, h, and i. Deglutition probably began in geniohyoideus sometime around pulse e so that its onset is confused by the simpler reflex phenomena. Note depression of background activity and of elementary reflex (pulse g) following deglutition.

FIG. 7. Action of anesthetics on deglutition; dog (5 Dec. 1953). a: deep ether; b: 2 hours later, isolated encephalon; c: 5 minutes after b, isolated encephalon with 10 per cent anesthetic dose of nembutal. Background activity in middle constrictor is associated with respiration and is not present in sedated states.

FIG. 8. Unanesthetized medulla, dog (5 Dec. 1953), 33 minutes following section of cord at C1. Note inhibition of inferior constrictor background during greater part of mylohyoideus action.
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FIG. 9. Variation of amplitude and durations of swallowing activity in the anesthetized and unanesthetized states, dog (6 Dec. 1953). a: deep ether; b: isolated encephalon 2 hours and 20 minutes later.

FIG. 10. Inhibition of cricothyroideus action early in deglutition. As mylohyoideus firing terminates, the characteristic burst of action appears in cricothyroideus. Dog (12 Dec. 1953), light urethane anesthesia.

ticipating the main lead muscle action by as much as 40 msec. The theoretical significance of this margin of lead for neurons of the fifth motor nucleus is not yet apparent, but it seems unlikely to be accounted for simply on the basis of shorter conduction distances. The posterior digastricus is inhibited for 100 or more msec. during the early phase of deglutition and then either gradually resumes background activity, if present (Fig. 11), or goes on to fire a pattern rather similar to that seen in the middle constrictor.

No satisfactory records were obtained from the cricoarytenoideus posterior although it appeared to fire roughly in parallel with thyroarytenoideus.

2. Modifiability of swallowing pattern

Figure 5 of necessity represents the EMGs of the participating muscles to be of fixed duration. There was actually wide variation observed in the

FIG. 11. Inhibition of posterior digastricus during deglutition. Monkey (1 Dec. 1953), ether anesthesia. See text.
duration of activity in various muscles of the total synergy, depending upon the prevailing level of medullary excitation. In a deeply anesthetized animal remaining unstimulated for several minutes, the first swallow obtained may be very weak as recorded mechanically (1, 4). Correspondingly, activity in the lead muscles may by 100 msec. shorter and of lower amplitude than that obtained after the animal is aroused and several swallows have ensued. For example, mylohyoideus may fire only 200 msec. in the unaroused, anesthetized animal, but for 300 msec. after arousal. In the unanesthetized preparation the mylohyoideus may fire for over 500 msec., but the seemingly more normal action in the lead muscles in the unanesthetized animal was about 400 msec. (Figs. 7, 8, 9) and it was this type of preparation on which the schema of Fig. 5 was based.

The temporal pattern of action among the different muscles is little disturbed by these variations of overall duration (Figs. 7, 9). In these instances, swallowing is prolonged or shortened as a whole—a temporal arrangement analogous to the spatial relation between points on a uniformly expanding or contracting surface, leaving proportionality unchanged despite quantitative variance. Thus, the peak activity in the middle constrictor in Fig. 7 falls just as mylohyoideus action is ending, despite the fact that the latter varies from 280 to 500 to 400 msec. duration under the three conditions. Similarly in Fig. 9 duration of thyrohyoideus action and lag period varies pari passu with timing of the mylohyoideus. In this example the duration of mylohyoideus action increases from 320 to 420 msec., while thyrohyoideus increases from 280 to 350 msec. and the lag in onset of its action from that in mylohyoideus increases from 66 to 100 msec.

Though the foregoing is the general rule, not all “temporal expansions” preserved the expected phase relations. For instance, pairing palatoglossus with thyroarytenoideus in the etherized monkey in the first swallow after several minutes of inactivity, the durations of activity were 260 and 190 msec. respectively, with thyroarytenoideus lagging by 40 msec. The second swallow, 14 sec. later, gave 300 and 240 msec. with 25 msec. lag; and a third, 7 minutes after removal of ether, gave 370 and 260 with thyroarytenoideus starting to fire concurrently with glossopharyngeus. Thus, in this case, it seems glossopharyngeus activity was lengthened by continuation after thyroarytenoideus activity had ceased while thyroarytenoideus firing was lengthened by earlier onset.

It is important to note that these conditions which generally cause so little rearrangement in the temporal organization of deglutition do greatly alter the amount of excitation necessary for its elicitation. For the swallows illustrated in Fig. 7, that of b in the unanesthetized state was evoked after only 12 volleys in SI (at a rate of 30/sec., liminal intensity), while in c, after 2.5 mg./kg. of intravenous nembutal (10 per cent of the anesthetic dose), 66 volleys were required. That in Fig. 7, a, under deep ether anesthesia, required 240 volleys. Under deep nembutal anesthesia, 1000 volleys may be needed to arouse the swallowing center. The drastic alteration of
neural action so evidenced is not found in the efferent time relations of the elicited swallow. There thus appears to be a high degree of stability in the efferent mechanisms of deglutition. This was further borne out by the failure of strychnine (0.2 mg./kg.) or moderate asphyxia (1-2 min.) to alter the organization save through minor changes in amplitude and duration of individual muscle activations.

No difference in temporal pattern, duration or amplitude could be found in swallows evoked by various means, including SL stimulation at frequencies of 3-100/sec., stimulation of the pharynx with a cotton swab or rapidly injected water, or swallows occurring without attempted experimental elicitation. The only exception was an isolated observation in which a "bolus" of rubber tubing or of cotton produced a greatly prolonged (800 msec.) activity. However, in this instance, neither a gagging nor an ejection response could have been differentiated from swallowing, as recording was only of the geniohyoideus and thyrohyoideus muscles.

All other attempts to modify the course of deglutition failed. The temporal organization of swallowing was unaltered by fixation of the hyoid mass at extreme rostral or caudal positions, varying degrees of traction upon the tongue, holding the mouth open, or placing head and neck in any extreme position. The exception was that of occasional slight enhancement of action in certain muscles. Participating muscles could be excised or procainized without affecting the sequence of events in the others; nor did concurrent stimulation of hypoglossal or lingual nerves change the response in any but the muscles which they innervate. Cocainization of surface of the pharynx did not alter swallowing evoked by SL stimulation.

3. Detailed pattern of electromyographic activity

While the temporal coordination of deglutition was constant, the action of individual motor units discernible with CRO recording was completely unpredictable. No two EMGs of deglutition from the same electrodes gave identical or even similar unit patterns. Some of this variation from one swallow to the next could perhaps be attributed to slight displacements of the electrodes accompanying motion of the muscles, so that in many instances the electrodes may not have sampled the same units from the same position each time. Nonetheless, it seems highly unlikely that the electrodes would never record the same units twice, and indeed the same units could frequently be identified throughout a long series of swallows. This variability in pattern of unit response is thus thought to reflect randomization of motoneuron discharge to the excitation emanating from the neural system regulating deglutition.

In the muscles showing most abrupt onset of swallowing activity, a period of some 50-100 msec. of recruitment is seen during which irregular firing of a few units increases into a massive discharge obscuring all details. The activity is similarly terminated in a gradual subsidence rather than by abrupt cessation. Thus, with the technique employed, it is only during onset
and termination of swallowing action in a particular muscle that unit behavior may be observed.

The complexity of the activation mechanism of deglutition previously described (1) was again manifest in the observation that in no experiment could a constant temporal relation be found between stimulus pulses and beginning of activity in lead muscles. This relation could be best studied using low frequencies of stimulation (3–10 pulses per sec.), in which the ensuing swallow is most likely to be directly linked with the pulse immediately preceding it rather than with an antecedent pulse. Thus, for example, in the etherized monkey with continuous SL stimulation at 5/sec. measurements on a series of swallows showed 170, 110, 170, 130, 160, 190, 170, 180, 70, and 135 msec. intervals between preceding pulse and beginning of EMG in mylohyoideus, while at 10/sec. the figures were 80, 30, 40, 65, and 90 msec. This temporal randomization and lag between input and output, extensively confirmed in all species, shows the intricacy of the processes converting spaced, synchronous volleys into the protracted and highly organized excitation delivered by the mechanism governing deglutition.

SL stimulation also evokes a variety of brief reflexes which follow stimulus pulses at consistent latency. These have been designated “elementary” reflexes to distinguish them from the more elaborate reflex performance of swallowing. These simpler reflexes were seen most frequently in geniohyoideus, palatopharyngeus, thyrohyoideus, cricothyroideus, and thyroarytenoideus and never in intrinsic muscles of the tongue. They were characteristically of low amplitude and highly inconstant pattern. Their minimum latency of 8–10 msec. seems to indicate that more than one synapse is involved even in these elementary reflexes. In ancillary studies, it was found that electrodes in fasciculus solitarius recorded potentials closely associated
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with the elicitation of deglutition within 1.0–1.5 msec. after SL stimulation (2). On the basis of this observation, and with the distances involved, no more than 5 msec. seems reasonable for conduction time and this, plus an additional msec. for neuromuscular transmission, leaves 2–4 msec. central delay. The multi-synaptic interpretation is consistent with Szentágothai’s failure to find monosynaptic linkages in the medulla save in masticatory and hypoglossal nuclei (9).

Further evidence of their complexity can be seen in Fig. 13. Here stimulation at 3/sec. elicited no reflex until the 12th and 13th pulses (a, b) at a latency of 12 msec. By the 25th pulse (d), the latency has shortened to 10 msec. and the reflex discharge is more prolonged and of larger and more vari-

![Fig. 13. Vocal cord reflex to contralateral SL stimulation, monkey (30 April 1954). a–d continuous stimulation at 3/sec., being the 12th on which the reflex appeared for the first time, 13th, 14th, and 25th pulses, respectively. e at 10/sec., f and g at 30/sec. The last half of thyroarytenoid activity in deglutition is seen in g followed by period of depression in which elementary reflex is lost or delayed (compare with f). Time 500/sec. for a–g.]

able amplitude. At moderate frequencies (e, f) the amplitude and complexity are increased. Of particular interest is the complete loss of the reflex immediately following deglutition (g; compare with record f immediately prior to this swallow) and its return, highly attenuated, with a 16 msec. latency. This was a typical finding and is equally well-illustrated for another muscle and another species in Fig. 6. These elementary reflexes are also commonly followed by a silent period of 30–40 msec., as can be seen readily in geniohyoideus (Fig. 6) having a high level of background activity. At stimulus frequencies above 30/sec. background in the geniohyoideus is thus fully obliterated.

Interaction between the elementary reflexes and deglutition is minimal. With low-frequency stimulation, a curtailed silent period associated with the stimulus pulse can frequently be observed during deglutition, as is suggested in Fig. 6. However, swallowing action proceeds unaffected by the
elementary reflexes at 30/sec. Thus, occupation of the motor nuclei by the elementary reflexes does not significantly modify the more complex synergies.

4. Respiration and other synergies

By reason of the continual nature of respiration, and the utilization of common pharyngeal passages, the synergies of swallowing and respiration must inevitably interact. There is a tendency for swallowing to occur uniformly at certain phases of the respiratory cycle. In dog and monkey, under ether or urethane anesthesia, approximately 80 per cent of the swallows occur during or at the peak of inspiration. In such instances, the action of the diaphragm continues unabated for 50 to 200 msec. after onset of activity in muscles of the leading complex (Fig. 12a). Occasionally and unpredictably, swallowing occurs under these conditions entirely during the expiratory cycle. In the cat under all conditions or in dog and monkey under nembutal anesthesia or during extreme respiratory suspension effected by SL stimulation, swallowing is usually associated with expiration. The widely reported, brief, isolated contraction of the diaphragm midway in deglutition (the "Schluckatmung") was observed only rarely and presumably is thus not an integral part of deglutition.

In early asphyxia most or all of the muscles active in deglutition are recruited into the respiratory effort. As a generality, the palatopharyngeus, posterior tongue, geniohyoideus, middle constrictor, and cricothyroideus are active during inspiration, while thyroarytenoideus, inferior constrictor, and thyrohyoideus (except in the cat) fire during expiration. Such action is usually of less amplitude than that seen in deglutition. It does not always fall in exact phase with respiration. Thus, the cricothyroideus and middle constrictor consistently fire 40 or more msec. before the diaphragm becomes active and cease correspondingly sooner. It is noteworthy that certain muscles firing in a parallel fashion under the influence of the respiratory center, as the two just mentioned, are active in different sequence during deglutition. Furthermore, respiratory action of middle constrictor can be abruptly inhibited with onset of deglutition, whereas the diaphragm frequently continues firing.

In the isolated encephalon under artificial respiration, the "respiratory" action of these muscles follows in proper phase with the expansion of the lungs, presumably through the mediation of the Hering-Breuer reflexes. Such influences are not, however, sufficient to preserve the uniformity of temporal relation normally expected between swallowing and the respiratory cycle, and in such cases swallowing occurs randomly in relation to artificial, "driven" respiration.

With incomplete asphyxia it is frequently seen, particularly in the monkey, that action ceases in the diaphragm after 1.5–2.0 min. while swallowing is still readily elicitable in normal pattern and cyclic respiratory efforts continue in the pharyngeal muscles. Diaphragm activity may reappear
later during gasping. One of the first asphyxial alterations of deglutition is the attenuation or disappearance of geniohyoid action. This occurs at a time when geniohyoid response in respiration is extremely vigorous, and, therefore, does not reflect a deterioration of motoneurons. Another differentiation between swallowing and respiratory influences is that produced by nembutal. As seen in Fig. 12c, even 10 per cent of the anesthetic dose causes considerable alteration in the respiratory pattern, but is without effect on the organization of deglutition.

Synergies of the pharynx other than swallowing and respiration were incidentally observed, but none other than respiration interacted directly with deglutition. Retching is particularly elicitable in the monkey and is characterized by sustained action for 1 sec. or more in the diaphragm, muscles of the larynx, the leading complex of swallow, and in the sternohyoideus and sternothyroideus, which are silent in deglutition. The synergy is distinguished from deglutition not only by its longer time course and recruitment of additional muscles, but by a different sequential arrangement in the firing pattern. Thus, the laryngeal muscles lead in retching, activity appearing in thyroarytenoideus 400 msec. prior to that in glossopharyngeus.

Licking antecedent to swallowing is very common in the cat. This event is marked by about 150 msec. activity in the entire tongue and geniohyoideus, more intense than that seen in swallowing, while other muscles remain silent (Fig. 6).

**Discussion**

Stimulation of afferents in the pharyngeal area is pluripotential, deglutition being but one of several effects obtainable. In addition, there is evoked a variety of simpler reflexes, general arousal of the animal and such electromyographically separable synergies as intra-oral manipulation, emesis, and effortful respiration (see Fig. 4). The manner of representation of these performances within the complex arrangement of the brain stem is still unknown. Since the early German explorations of the problem (e.g., 5, 6, 8, 12), it has been customary to assume deglutition to be controlled by an ill defined "center." The term will be adopted in the present discussion to signify what is probably an anatomically diffuse group of neurons interposed between afferent and efferent systems and so inherently linked that their excitation will automatically invoke motor activity in the full spatio-temporal sequence of swallowing. Deglutition might be represented in such a system either in a unitary fashion or as a hierarchy of separable subsynergies. Alternatively, the integration could be accomplished by collateral linkages between motoneurons, or sequentially activated by afferents from earlier performing muscles. The first definitive evidence on the manner of this organization was obtained by Wassilieff (12) and confirmed by Markwald (5). They showed that section of the brain stem at the pontine level excluded mylohyoideus action while not obviously modifying the course of deglutition. It thus seems unlikely that swallowing could be organized solely...
by sequential linkages between motor pools. It is possible, of course, that the other remaining muscles of the leading complex might continue to initiate such a successive activation.

Other evidence opposing organization by motoneuron collaterals was obtained in the experiments here reported. In monkey or cat during asphyxia there is an attenuation of activity in the geniohyoideus in swallowing compared with its performance in respiration. In this circumstance, which is functionally comparable to the anatomical excision noted above, the thyrohyoideus action continues in full amplitude in both performances. It is improbable that different motoneurons of the geniohyoideus are involved in these two synergies, or that the increased activation of this muscle in respiration should diminish the responsiveness of its motoneurons in swallowing. Rather, this local differentiation of amplitude of response during asphyxia would indicate variation in effect upstream to the motor pool. This dissociation would further imply that the "center" governing swallowing is composed of fractions having different degrees of activation in asphyxia.

On the other hand, the extraordinary consistency of the motor pattern of deglutition demands a unitary, stable regulatory system. This is perhaps attained in some degree by the arrangement which makes the ultimate performance of the center independent of peripheral modifications. Thus, while it is conceivable that following its initiation the course of deglutition would be regulated by continuing exteroceptive and proprioceptive stimuli, experiment has failed to detect such an effect. Cocainization of the pharynx, or transection or procaine infiltration of various participating muscles, left the general pattern of activity unaltered. Such evidence indicates deglutition to be centrally controlled and autonomous of afferent support. This could be unequivocally demonstrated only with neuronal rather than EMG recording from the completely curarized animal with exteroception eliminated by local anesthesia. The conclusion suggested here, however, gains some support from reports of the absence of proprioceptive fibers or receptors in many of the muscles concerned in deglutition (reviewed in 11).

In this apparent independence from proprioceptive modification, deglutition differs conspicuously from posture and simpler motor functions of trunk and limbs. The crossed extensor reflex is modified by position of the limbs involved. Limb muscle response to motor cortex stimulation is altered by changing resting posture (3). The frequency of shivering movements is dependent upon muscle tension (7). No such effects have been observed for deglutition, and it is likely such afferent control would be inappropriate in a muscular region performing in a variety of necessarily independent synergies.

The efferent stability of the swallowing center is striking in comparison with the marked variation in its threshold to stimulation by the afferent influences to which it is accessible. Depending upon level of anesthesia, there is more than a 20-fold variation in threshold to SL stimulation. De-
spite this variation, the pattern of deglutition remains unaltered. It is widely agreed that barbiturates may selectively depress multisynaptic channels and what is generally termed "internuncial activity." The spontaneous activity of the unanesthetized medial reticular formation of the medulla, presumably representing such internuncial discharge, is almost abolished by only 25 per cent of an anesthetic dose of nembutal (2). The depression of evocation of deglutition implies an internuncial arrangement at the afferent portal of this coordinative mechanism, as previously reported (1), and anesthesia probably lowers the excitability of the motor pool (see Figs. 7, 9). Yet Fig. 12 illustrates the constancy of swallowing during barbiturate sedation sufficient to alter respiration greatly. This lack of anesthetic depression is difficult to explain, for current neurophysiological concepts would indicate that the coordination sustained for hundreds of msec. in deglutition among irregularly dispersed neural groups could be achieved only through extensive interneuronal action. If this be true, then it must be assumed that many neurons of the swallowing center are highly resistant to anesthetic action.

The inhibitory components of the pattern of deglutition are of interest, for they demonstrate a further element of complexity in the controlling system. Since no consistent reciprocal relations were observed among any of the participating muscles, the inhibitory action must, like the excitatory, be thought of as proceeding from a swallowing center. The inhibition seen during the early stages of deglutition in thyrohyoideus, thyroarytenoideus, cricothyroideus, middle and inferior constrictors, and posterior digastricus is a prominent feature of the swallowing pattern (Figs. 5, 7, 8, 9, 10). A silent period following swallowing action is clearly demonstrated by a diminution of both elementary reflexes and of background activity (Figs. 6, 13). Though it is difficult to gauge the intensity of motoneuron activity pursuant to deglutition, a condition of subnormality or fatigue following such action seems unlikely to account for this prolonged silent period. If the observed depression is an active inhibition, then the attenuation or abolition of the pauci-synaptic elementary reflexes indicates this inhibition must be exerted in close connection with or at the motoneuron. Such inhibition could, of course, equally well represent adjacent respiratory action.

Summary

The electromyographic pattern of activity of deglutition was observed in 22 muscles in the area of mouth, pharynx, and larynx of monkey, cat, and dog. While such motor units as could be identified seemed to fire an unpredictable and random pattern from one swallow to the next, the overall schedule of excitation and inhibition among the participating muscles was highly constant. No difference in temporal pattern, duration or amplitude could be found in swallows evoked by various means including superior laryngeal nerve stimulation at frequencies of 3–100/sec. and stimulation of the pharynx with a cotton swab or rapidly injected water.

A "leading complex," consisting of the superior constrictor, palato-
pharyngeus, palatoglossus, posterior intrinsic muscles of the tongue, stylo-
glossus, stylohyoideus, geniohyoideus, and mylohyoideus, fire concurrently
for 250–500 msec. to initiate the act. Other muscles, such as the middle con-
strictor, thyrohyoideus and thyroarytenoideus, are inhibited at the onset,
becoming active after varying delays. Action in the inferior constrictor is
deferred until leading muscle action is nearly over. There is no great species
variation save in the muscles of the larynx. Sternothyroideus, sternohyo-
deous, intrinsic muscles of the anterior tongue and digastricus of cat and dog
are silent in deglutition but they participate in other synergies such as lick-
ing, chewing, and emesis.

A variety of elementary reflexes were observed to follow stimulus pulses
to the superior laryngeal nerve at a minimum latency of 8–10 msec., but
no consistent temporal relation could be established between such pulses
and onset of deglutition.

Procainization, stretch or transection of various participating muscles,
cocainization of the pharynx, and administration of strychnine, anesthetics
or moderate asphyxia all failed to effect substantial alteration of the pattern
of deglutition.

The results are discussed in relation to possible mechanisms organizing
this coordination. The electromyographic evidence is incompatible with a
system requiring continued afferent regulation or collateral linkages between
motor nuclei.

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