EMG of the Digastric Muscle in Gibbon and Orangutan: Functional Consequences of the Loss of the Anterior Digastric in Orangutans

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ABSTRACT Unlike all other primates, the digastric muscle of the orangutan lacks an anterior belly; the posterior belly, while present, inserts directly onto the mandible. To understand the functional consequences of this morphologic novelty, the EMG activity patterns of the digastric muscle and other potential mandibular depressors were studied in a gibbon and an orangutan. The results suggest a significant degree of functional differentiation between the two digastric bellies. In the gibbon, the recruitment pattern of the posterior digastric during mastication is typically biphasic. It is an important mandibular depressor, active in this role during mastication and wide opening. It also acts with the anterior suprahyoid muscles to move the hyoid prior to jaw opening during mastication. The recruitment patterns of the anterior digastric suggest that it is functionally allied to the geniohyoid and mylohyoid. For example, although it transmits the force of the posterior digastric during mandibular depression, it functions independent of the posterior digastric during swallowing. Of the muscles studied, the posterior digastric was the only muscle to exhibit major differences in recruitment pattern between the two species. The posterior digastric retains its function as a mandibular depressor in orangutans, but is never recruited biphasically, and is not active prior to opening. The unique anatomy of the digastric muscle in orangutans results in decoupling of the mechanisms for hyoid movement and mandibular depression, and during unilateral activity it potentially contributes to substantial transverse movements of the mandible. Hypotheses to explain the loss of the anterior digastric should incorporate these functional conclusions.

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The orangutan is distinguished from other extant primates by the absence of an anterior digastric and by the insertion of the posterior digastric onto the mandible near the gonial angle (Brown, 1989; Brown and Ward, 1988; Chapman, 1880; Sonntag, 1924; Winkler, 1991). Since the anterior digastric, the inferior head of lateral pterygoid, and the geniohyoid are generally considered to be the most important jaw openers in primates (e.g., Aiello and Dean, 1990; DuBrul, 1980; Hylander et al., 1987), the loss of the anterior digastric may be far from trivial.

Several explanations for the loss of the anterior digastric in orangutans have been suggested. Cachel (1984) suggests that the mass of the orangutan’s mandible is sufficient to let gravity depress it. However, as Winkler (1991) notes, the gorilla has a mandible that is as massive as the orangutan’s yet retains both bellies of the digastric.

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Brown and Ward (1988:253) suggest that the prominent submandibular expansion of the laryngeal air sacs of orangutans is correlated with the absence of the anterior belly, and that the air sacs may “render the standard suprahypoid muscle pattern untenable.” They add that many primates have expanded air sacs, but the submandibular position is distinctive of orangutans. Although this hypothesis is difficult to falsify, it should be noted that the large submandibular air sacs of the siamang are nearly identical to those of the orangutan, both topographically and anatomically (in that the left and right sacs fuse to form a single sac, Negus, 1949; pers. obs.), yet it has an unmodified digastric muscle. Most recently, Winkler (1991) has proposed that both dietary specializations and hyolaryngeal modifications in orangutans may have led to the loss of this muscle belly or its fusion with the adjacent mylohyoid.

Most mammals have a two-bellied digastric muscle, often connected in some fashion to the hyoid bone (Chaine, 1907; Jouffroy et al., 1968 and references therein; Turnbull, 1970; Weijs, 1973). Although orangutans are, to our knowledge, the only species to lose the anterior belly, the posterior belly is absent in cetaceans, pigs, and lagomorphs (Bijvoet, 1908; Jouffroy et al., 1968; Muhl, 1982; Weijs et al., 1987). In these animals, the anterior digastric inserts onto the basi-cranium via a long tendon.

The rarity of one-bellied digastric muscles suggests the hypothesis that the two parts of digastric may be differentiated functionally to some extent. If there were no functional differentiation, we would expect more species to adopt the less costly option of growing, maintaining, and contracting a single muscle belly. A test of this hypothesis requires knowledge of the activity patterns of both bellies during feeding behaviors. However, in humans, macaques, and other species that have a bipartite digastric, only the anterior belly has been studied in detail (e.g., Dotsch and Dantuma, 1989; de Gueldre and de Vree, 1989; de Jongh et al., 1989; Hylander et al., 1987; Juniper, 1981; Kallen and Gans, 1972; Luschei and Goodwin, 1974; McNamara, 1973a,b; Möller, 1966; Moyers, 1960; Vitti and Basmajian, 1977; Weijs and Dantuma, 1975). An exception is the study by Crompton et al. (1975) on the EMG activity of the hyoid muscles during mastication in the opossum. Their data suggest that the anterior and posterior digastric are both involved in hyoid elevation and mandibular depression during jaw opening, but that the opossum’s posterior digastric is recruited independently of the anterior digastric during the power stroke, coincident with the initial elevation of the hyoid.

Here we compare the EMG activity patterns of the digastric muscle and several other potential mandibular depressors in the gibbon and the orangutan. The aims of this study are to evaluate the hypothesis that the digastric bellies are functionally differentiated in the gibbon and to gain insight into the functional consequences of the unique arrangement of the digastric muscle in the orangutan. We ask the questions: If the anterior digastric is an important mandibular depressor, how has the orangutan managed to survive the loss of this muscle, or if the anterior digastric is not critical for mandibular depression, then what (if any) function has been lost or altered in the orangutan?

**MATERIALS AND METHODS**

Subjects for the electromyographic study were one subadult (7.5 years, 24 kg) male orangutan (*Pongo pygmaeus*) possessing a nearly complete adult postcanine dentition (M3s erupting) and one adult (20 years, 6 kg) male white-handed gibbon (*Hylobates lar*) that had no canine teeth and worn molar teeth, but otherwise a complete dentition. In the orangutan, we studied the inferior head of the lateral pterygoid (ILHP), posterior digastric, geniohyoid, and superficial masseter muscles (Fig. 1A). In the gibbon, we studied the ILHP, anterior digastric, posterior digastric, mylohyoid, geniohyoid, and superficial masseter muscles (Fig. 1B). Dissections were performed on two gibbons and one orangutan in order to determine the best approach for electrode insertion.

A fine-wire bipolar electrode was implanted into each muscle with a 25-gauge hypodermic needle while the subject was
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movements produced (see Results, Muscular Stimulation for details). In the gibbon, the needle was inserted into the anterior digastric approximately 5 mm lateral to the midline just deep to the skin and platysma, and for the posterior digastric the needle was inserted immediately superior to the junction of the greater horn and body of the hyoid and directed craniodorsally along the direction of the muscle. In the orangutan, the needle was positioned posterosuperior to the gonial angle and directed upward and backward along the length of the posterior digastric.

For both subjects, the IHLP was accessed by opening the jaws so that the space bounded by the inferior border of the zygomatic arch, the condylar process of the mandible, and the coronoid process of the mandible was enlarged. The needle was positioned anterior to the condylar process and inserted into this space, through the masseter and temporalis, to implant the electrode into the IHLP.

The geniohyoid is a thick muscle lying deep to the mylohyoid. In the orangutan, it was accessed by inserting the needle to a depth of 1 cm, approximately 1 cm lateral to the midline on the underside of the mandible. In the gibbon, the needle was inserted to a depth of approximately 6 mm at a site approximately 5 mm lateral to the midline of the neck, just anterior to the body of the hyoid.

There was the possibility that an electrode placed in the geniohyoid might displace into the space between the geniohyoid and mylohyoid, or even onto the superficial surface of the mylohyoid. Unfortunately, when we considered this possibility, the orangutan was no longer available for study. In the gibbon, we were able to record from the mylohyoid, and EMG activity in this muscle was used to evaluate the integrity of the geniohyoid electrode. To implant an electrode into the mylohyoid, the needle was inserted just anterior to the hyoid body, deep to the platysma. The insertion sites for both the geniohyoid and mylohyoid in the gibbon offered the advantage of being able to implant electrodes into these muscles without passing through the anterior digastric (Fig. 1B). With this approach, therefore, we

under halothane/nitrous oxide anesthesia. Proper initial electrode positioning was verified by sending a small (200–500 μA) sinusoidal current back through the electrode and observing the muscle contraction and/or

Fig. 1. A: Lateral view of skull of Pongo pygmaeus showing the muscles studied. Note the mandibular insertion of the posterior digastric. IHLP = inferior head of lateral pterygoid. B: Lateral view of skull of Hyllobates lar showing the muscles studied. C: Ventral view of the submandibular region of H. lar. Note the aponeurotic insertion of the anterior digastric onto the hyoid body. See text for discussion.
could be confident of collecting separate recordings of each of the anterior suprahyoid muscles.

Electrode placement in the superficial masseter was straightforward in both subjects, the needle being inserted near the anteroposterior midpoint of the muscle.

The analysis is based on 28 recordings. For the gibbon, these included two of the posterior digastric, one of the IHLP, six of the superficial masseter, seven of the anterior digastric, two of the geniohyoid, and two of the mylohyoid. For the orangutan, we obtained three recordings of the posterior digastric, one of the IHLP, three of the superficial masseter, and one of the geniohyoid. The duration of a recording session ranged from 15 minutes to 1.5 hours, and we collected large samples of the EMGs for each muscle in each experiment. In those cases for which two or more recording sessions were available for a muscle, intraindividual variability appeared to be minimal, except where noted in the text.

The techniques used for EMG data collection are the same as those given in Larson et al. (1991) for use on locomotor data. The electrodes were connected to a four-channel telemetry transmitter pack attached to a lightweight harness worn by the subject. The pack transmitted EMG signals from four electrodes to an FM receiver, which relayed them to an oscilloscope. A video camera aimed at the oscilloscope screen recorded the EMG traces, and this image was superimposed by a special effects generator onto a videotape record of the subject's face recorded by a second video camera. After each sweep of the oscilloscope beams, the video picture of the subject was electronically eliminated for 0.1 second, leaving a clear image of the EMG activity during the preceding interval. This image was copied onto paper by a video hard copy device in order to collect records of the EMG patterns observed during particular behaviors.

The subjects were not restrained in any way, and they fed themselves during a recording session. Usually, the subject remained seated during a session. Simultaneous recording of the EMG signals and the face of the subject in either the frontal or lateral view allowed the correlation of the position of the mandible with muscle activity. The majority of the data were recorded with a frontal view of the subject. Balancing and working sides were identified based on the direction of jaw movements in the frontal view chewing cycles.

Data analysis was carried out using frame-by-frame playback (30 frames/sec) of a videotape record of a recording session. Jaw movements and other behavioral activities were noted on the hard copy of the electromyogram.

The face and neck of each subject were shaved to enhance visual identification of jaw movements. Opening during mastication was defined as beginning at the frame where depression of the mandible was first observed and ending at maximum gape for that cycle. In the gibbon, slow and fast opening were identified qualitatively by a frame-by-frame assessment of change in gape over time. Closing as used in this analysis includes both the closing and power strokes.

In the gibbon, recognition of the pattern of anterior suprahyoid muscle activity during swallowing initially occurred when the subject went through long (5–20 minutes) periods of time without eating. During these times, we recorded periodic (every 20–60 seconds) bursts of activity in the anterior suprahyoid muscles that occurred while the subject's mouth was closed and were of longer duration than the activity seen in these muscles during mandibular opening. These observations were supplemented occasionally by visual detection of laryngeal elevation while the mouth was closed. We concluded that these bursts were associated with the deglutition of saliva. Using this prolonged pattern of activity as a guide, food swallows, both within chewing sequences during brief pauses in rhythmic jaw movement and at the ends of chewing sequences, could be distinguished easily from muscular

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Because gibbons and orangutans are difficult to acquire as experimental subjects, this study is based on only one subject of each species. While we believe that the basic phasic nature of a muscle's activity pattern will be accurately represented by a single individual, we obviously cannot comment on those aspects of muscle recruitment that are likely to reflect intraspecific variation, such as minor differences in onset-offset time and speed of contraction (e.g., Hylander and Johnson, 1993; Weijs and Muhl, 1987).
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activity during jaw opening. Swallowing in the orangutan was identified only at the ends of chewing sequences (see Results, Orangutan).

A variety of other behavioral activities (e.g., wide opening, incision, licking) were recorded. Voluntary wide opening was defined as mandibular depression in order to accommodate an object of greater than 4 cm in the mouth. Wide opening prior to incision included gapes that were larger than the largest gape attained during chewing. Comparisons of the amplitudes of the EMG signals for different activities were made only when the activities occurred during the same experiment (Nandedkar and Sanders, 1990).

The orangutan was recorded eating carrot sticks, quartered apples with skin, whole apples with skin, celery stalks, plums, bananas, almonds, marshmallows, and gummy bears. The gibbon ate pieces of banana, plum pulp, apricot, and prune, each of which were incised from whole fruit, as well as apple pieces, almonds, and raisins.

For part of the analysis, initial food item size was divided into large and small object categories. The orangutan incised very large pieces of food, and all food items (except almonds, marshmallows, and gummy bears) were placed in the large object category. The gibbon prepared much smaller pieces of food than the orangutan, and most items were placed in the small object category. However, the gibbon incised large pieces of banana, and these were categorized as large objects preceding the first swallow of a chewing sequence and small objects in all subsequent chewing cycles. Differences in muscular activity pattern between large and small object chewing cycles were compared statistically using the row-by-column G-test (Sokal and Rohlf, 1981).

RESULTS

Muscular stimulation

In both subjects, stimulation of the IHLP elicited pronounced mandibular depression, and stimulation of the superficial masseter caused mandibular elevation and protrusion. Stimulation of the gibbon's anterior digastric produced both mandibular depression and anterocranial displacement of the hyoid. Dissection revealed that the anterior digastric in gibbons attaches both to the intermediate tendon of the digastric muscle and aponeurotically onto the body of the hyoid (Fig. 1C). The intermediate tendons of the left and right digastric join to form a tendinous arc situated between the mandibular symphysis and the anterior border of the hyoid body. The aponeurosis of the anterior digastric is attached to the concave edge of this tendinous arc. Some of the anterior digastric fibers insert directly into the aponeurosis, but the majority attach to the tendinous arc. Laterally, the intermediate tendon is situated cranial to the junction of the body and greater horn of the hyoid, and is held in place at this junction by fascia (Fig. 1B). The fact that stimulation of the gibbon's anterior digastric produced anterocranial motion of the hyoid confirms that the aponeurosis connecting it to the hyoid body is capable of transmitting enough force to move the hyoid.

Stimulation of the posterior digastric produced mandibular depression and slight retraction of the mandible in both the gibbon and the orangutan. The absence of hyoid motion upon stimulation of the gibbon's posterior digastric correlates with the observation that the posterior digastric has no direct attachment to the hyoid. However, the sling holding the internodent to the hyoid (Fig. 1B) should permit coactivation of both bellies to produce hyoid elevation.

Stimulation of the gibbon's mylohyoid produced slight hyoid elevation and tongue protrusion. Stimulation of the geniohyoid in the gibbon elicited slight mandibular depression and marked elevation of the hyoid with tongue protrusion. Stimulation of the orangutan's geniohyoid also produced slight mandibular depression and tongue protrusion. We presumed the latter was related to hyoid movement. Hyoid movement was difficult to monitor in the orangutan due to the large air sacs and to the elevated rest position of the hyoid. Lateral radiographs confirm that the hyoid body in orangutans is located approximately at the lower border of the mandible (Fig. 2A). In the gibbon, the hyoid body is below the lower border of the mandible (Fig. 2B).
Fig. 2. A: Lateral radiograph of skull of an adult male *Pongo pygmaeus*. The hyoid body in its rest position (arrow) is located approximately at the lower border of the mandible. The hyoid was similarly positioned in two additional individuals. B: Lateral radiograph of skull of an adult male *Hylobates lar* (the EMG subject). In its rest position, the hyoid body (arrow) is inferior to the lower border of the mandible. The hyoid was similarly positioned in one additional individual.

**ELECTROMYOGRAPHY**

**Gibbon**

Simultaneous contraction of the anterior and posterior bellies of the digastric potentially affects both hyoid and mandibular movement. In order to distinguish recruitment related to hyoid motion from that related to mandibular depression, we first summarize the activity patterns of the ge-
Geniohyoid and mylohyoid and mylohyoid as more or less pure hyoid movers, and of the IHLP as a pure mandibular depressor. The activity patterns of the digastric muscle will then be reviewed within this context.

**Geniohyoid and mylohyoid**

The activity patterns of geniohyoid (Fig. 3) and mylohyoid (Fig. 4) were similar to one another in many respects. Both were recruited at low levels during wide opening (Figs. 3A and 4A). During mastication, recruitment of the geniohyoid (Fig. 3B) and mylohyoid (Fig. 4B) began prior to visible opening of the mandible, and their activity overlapped with that of superficial masseter. In lateral view, elevation of the laryngeal apparatus was visible at this time. Both muscles continued to be active during opening, and the activity of both diminished significantly at or near the end of slow opening. During contralateral chews, the mylohyoid displayed a second burst of activity that began during the preceding fast opening and occasionally continued into the early part of closing (Fig. 4B). This burst may be related to tongue movement during positioning of the food bolus and has also been observed in
humans (Møller, 1966). Both muscles displayed marked activity during swallowing episodes (Figs. 3C and 4C).

**IHLP**

Substantial activity in the IHLP occurred during wide opening of the mandible, and it was active for the duration of the opening movement (Fig. 5A). During mastication, low amplitude recruitment of the IHLP was usually initiated prior to visible mandibular depression, but well after the suprahypoid muscles began contraction (Fig. 5B). Activity in the IHLP continued throughout slow
and fast opening on both the balancing and working sides of the mouth. Although sporadic activity was occasionally observed during the early part of a food swallowing episode, the IHLP was recruited consistently only at the end of a food swallow (Fig. 5C). At this time, the subject’s mandible was depressed, either to continue chewing or to take another bite of food.

**Anterior and posterior digastric**

The two bellies of the digastric differed significantly in recruitment patterns. Recruitment of the anterior digastric was most similar to that of the geniohyoid, whereas the posterior digastric pattern was typically biphasic during mastication but similar to that of the IHLP during wide opening and swallowing.

During wide opening, anterior digastric activity was low level and variable (Figs. 4–6), like that of the other anterior suprahyoid muscles. In contrast, the posterior digastric, like the IHLP, consistently displayed high amplitude activity during wide opening (Fig. 6).

During mastication, both digastric bellies became active prior to visible mandibular depression (Fig. 7C). As shown in Figures, 4, 5, and 7, the duration of activity in the anterior digastric varied, and a diminution in amplitude often occurred during fast opening. Recruitment of the posterior digastric was characteristically biphasic, but the muscle displayed several recruitment patterns that varied significantly in association with food object size (Fig. 8). The G-test distinguished two large object patterns (1 and 2 in Fig. 8) from three small object patterns (3, 4, and 5 in Fig. 8) at $P < 0.05$. In addition, patterns 1 and 2 were distinct from each other and from patterns 3, 4, and 5 as a group at $P < 0.01$. These results indicated that continuous activity (pattern 1) occurred during large object cycles and prolonged silence during opening (pattern 3) occurred during small object cycles, but the predominant pattern for the posterior digastric was biphasic (patterns 2 and 3).

Contrast in the recruitment of the anterior digastric vs. the posterior digastric was perhaps most striking during swallowing episodes (Fig. 7). Like the geniohyoid and mylohyoid, the anterior digastric was recruited during swallows at very high amplitudes. The posterior digastric displayed minimal or no activity during most swallowing episodes, although slight to moderate activity occasionally occurred.

**Orangutan**

**Geniohyoid**

The geniohyoid was not recruited during wide opening, even during prolonged bouts of mandibular depression (Fig. 9A). During mastication, the geniohyoid was active during opening (Fig. 9B). Activity began either prior to or at the initiation of visible mandibular depression and often ceased prior to the end of the opening movement.

At the ends of chewing sequences, the geniohyoid exhibited activity of longer duration than that seen during rhythmic mastication (not shown). Presumably, this activity was associated with swallowing similar to that observed in humans (e.g., Hrycyshyn and Basmajian, 1972), macaques (Hylander et al., 1987; McNamara and Moyers, 1973), and the gibbon (see above).

**IHLP**

This muscle initiated voluntary wide opening of the mandible (Fig. 10A). During mastication, contraction of the IHLP was associated directly with mandibular depression (Fig. 10B). It was active during all of the recorded chewing cycles.

**Posterior digastric**

The activity pattern of the orangutan’s posterior digastric exhibited both differences from and similarities to that of the gibbon. As in the gibbon, the orangutan’s posterior digastric was recruited in concert with the IHLP. For example, the posterior digastric was maximally recruited during voluntary wide opening, although onset of activity usually lagged behind activity in the IHLP (Fig. 10A).

During mastication, the posterior digastric had a single burst of activity during opening (Fig. 10B). Unlike the gibbon, neither the working nor the balancing side
Fig. 5. EMG signals recorded in the anterior digastric, IHLP, and superficial masseter in gibbon. The food item is a banana. A: Wide opening prior to incision. B: Mastication with working and balancing side shift during sequence. This example shows an increase in amplitude in IHLP during fast opening. A uniformly high amplitude in the IHLP throughout opening was an equally common pattern. C: Swallowing episode. Abbreviations as in Figures 3 and 4.
Fig. 6. EMG signals from the posterior digastric, anterior digastric, and superficial masseter during voluntary wide opening in gibbon (maximum gape approximately 6 cm). Note the high amplitude of activity in the posterior digastric and compare it to Figure 7.

The EMG results provide support for the hypothesis that functional differentiation is present in the digastric bellies of gibbons. The most compelling evidence for this is that some behaviors are associated with significant recruitment of the anterior digastric, and insignificant or no recruitment of the posterior digastric, while other behaviors are accompanied by a predominance of posterior digastric activity and insignificant recruitment of the anterior digastric. Thus, in this study the independent function of a digastric belly is defined by behavior-specific, asymmetric recruitment. The data also suggest that in some circumstances the two bellies in gibbons have a common or shared function. In contrast, the recruitment pattern of the orangutan’s posterior digastric indicates that this muscle has a single function.

The independent function of the posterior digastric in gibbons and the single function of this muscle in orangutans is to depress the mandible. In the gibbon, the high amplitude of activity in the posterior digastric during wide opening contrasts sharply with the insignificant activity of the anterior digastric (or geniohyoid) during this movement. This suggests that the posterior di-
gastric provides active force promoting mandibular depression and that this force is transmitted through a weakly activated anterior digastric. Furthermore, recruitment of the posterior digastric is responsive to food object size during mastication in both subjects. This sensitivity may reflect different gape requirements in large vs. small object feeding. Finally, the posterior digastric in both subjects is largely inactive during most swallowing episodes.

In the gibbon, the shared function of the posterior and anterior digastric is to participate in moving the hyoid prior to jaw opening during mastication. At this time, both bellies are recruited with other anterior suprahyoid muscles that move the hyoid. This interpretation is straightforward because the mandibular elevator muscles (e.g., the superficial masseter, see Figs. 3, 5, and 7) prevent mandibular depression at this time.

Both the independent and shared roles of the posterior digastric in the gibbon are in evidence during mastication. The pre-opening burst corresponds to its participation in hyoid motion and the opening burst to its role in mandibular depression. Although hyoid movement probably occurs during the opening burst, activity in the posterior digastric is associated with an increase in the velocity of the mandible and diminution in the activity of the anterior digastric (Fig. 8). This association, and the observations discussed above, support the conclusion that the posterior digastric contributes more to mandibular depression than to hyoid movement at this time.

In the orangutan, the posterior digastric is not biphasic, lacking the pre-opening burst of activity that is seen in the gibbon. Instead, the posterior digastric is active only during jaw opening, and its unambiguous function is to depress the mandible. Because it is also a depressor in the gibbon, this appears to be a retained rather than a new function.

A comparison of digastric recruitment in the orangutan with that in animals lacking the posterior belly provides interesting functional contrasts. EMG studies (Haraguchi and Yamada, 1992; Herring and Scapino, 1973; Schwartz et al., 1989; Weij and Dantuma, 1981; Wejs and Muhl, 1987) indicate that, as in the orangutan, the retained digastric belly in lagomorphs and pigs functions to depress the mandible. However, the presence of substantial pre-opening recruitment suggests additional functions for the anterior digastric in lagomorphs and pigs (see also Anapol and Herring, 1989; Anapol et al., 1987; Muhl and Newton, 1982).

Based on similarities in the recruitment patterns of the gibbon's anterior suprahyoid muscles and their differences from those of the posterior digastric, we suggest that the anterior digastric is functionally allied to the geniohyoid and mylohyoid and functions as a protractor/elevator of the hyoid independent of the posterior digastric. This is most apparent during swallowing episodes when the anterior digastric is recruited without significant activity in the posterior digastric. As noted above, at other times the anterior digastric acts in conjunction with the posterior digastric, initially as a partner in producing hyoid movement during the pre-opening posterior digastric burst, and later to transmit the force of the posterior digastric to the mandible.

The comparative anatomical evidence is consistent with these interpretations. The anterior digastric has a direct, aponeurotic insertion onto the hyoid body in the gibbons we dissected. In African apes (Raven, 1950; Sonntag, 1923; Swindler and Wood, 1973) and in humans (Munro, 1973; Stern, 1988), the anterior digastric has a fleshy or aponeurotic insertion onto the hyoid body. The posterior digastric has no direct connection to the hyoid in gibbons or in African apes (Raven, 1950; Sonntag, 1923; Swindler and Wood, 1973), although in humans it may have a link to the hyoid arising from the intertendon (Munro, 1973). These observa-

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**Fig. 7.** EMG signals from the posterior digastric, anterior digastric, and superficial masseter during swallowing episodes in gibbon. A: Typical activity pattern during food swallow (N = 56). B: Typical activity pattern during saliva or food swallow (N = 25). C: Slight to moderate activity observed in the posterior digastric during food swallow (N = 28) followed by opening and closing strokes. Note the biphasic pattern in the posterior digastric during chewing. Abbreviations as in Figure 3.
Fig. 8. Diagrammatic representation of the activity patterns in the gibbon’s anterior and posterior digastric. Histograms give the number of large and small object cycles for which each pattern occurred. A triphasic (pre-opening, slow opening, and fast opening bursts) pattern occurs infrequently in the posterior digastric, and such activity was placed into Pattern 1. See text for discussion.
A Wide Open

Right Geniohyoid

1 mV

1 sec

C O

Fig. 9. EMG signals recorded in the geniohyoid in orangutan. The food item is a banana. A: Wide opening. B: Mastication, working side muscles. Note the variation in onset and offset times. C = closing; O = opening.

...tions indicate that extant hominoids, with the exception of orangutans, may be characterized by a degree of functional independence of the digastric bellies. The ability of the posterior digastric to move the hyoid without co-contraction of the anterior digastric is probably minimal, as revealed by our observations on stimulation of the posterior digastric in the gibbon.

Functional differentiation of the digastric bellies in the gibbon may be related to the coordination of hyomandibular movements. In mammals, hyomandibular movements are smoothly integrated during mastication, and anterocranial movement of the hyoid relative to the mandible is characteristic of the power stroke and the early part of opening (Anapol, 1988; Crompton et al., 1975; German and Franks, 1991; Thexton et al., 1982). This results in coordinated movement of the teeth and tongue so that food can be prepared, transported, and swallowed (Hayenga and Hiemae, 1993; Hiemae et al., 1978; Thexton and McGarrick, 1988). In humans, the hyoid bone is protracted (Palmer et al., 1992; Thexton et al., 1976) and elevated slightly (Pancherz et al., 1986) prior to and during slow opening. It is retracted late in opening and during fast closing (Palmer et al., 1992; Thexton et al., 1976). Palmer et al. (1992) identify the suprahyoid muscles as the protractors and the infrahyoid muscles as the retractors in humans. Hyoid movements in macaques are similar to those of humans (Franks et al., 1984; Hiemae and Palmer, pers. comm.).

The absence of the anterior digastric has not altered the orangutan's ability to open its mouth, since the posterior digastric is retained as an important mandibular depressor. However, the loss of the anterior digastric in orangutans has several functional consequences. In contrast to other primates, the posterior digastric inserts laterally, that is, onto the gonial angle, in orangutans. In addition to opening the mouth, the orangutan's posterior digastric should act to regulate the motion of the ipsilateral condyle by pulling the mandible upward and backward. This may give it the ability to assist the contralateral IHLP in deviating the mandible. We observed marked transverse movement of the mandible during opening in the orangutan subject and suggest that the sequential recruitment of the mandibular depressors (working side IHLP, balancing side posterior digastric, 

\footnote{The contribution of the posterior digastric is unknown. Munro (1974) described a biphasic pattern for the human posterior digastric. However, activity is very low in amplitude and the muscle appears to have been continuously active (e.g., Munro's Figs. 3, 4, and 6). The latter suggests that there was not a pure signal from the muscle or that the use of a needle electrode elicited a pain response (spasm). For these reasons, the data are not directly comparable to those for the gibbon.}
balancing side IHLP, working side posterior digastric) and the lateral insertion of the posterior digastric were responsible for these movements.

Another consequence of losing the anterior digastric is that the geniohyoid is the primary protractor of the hyoid. Orangutans have an elevated hyoid relative to the lower border of the mandible compared to that of gibbons (Fig. 2). Although this is not unique among primates (Fink, 1975), the location of the hyoid at rest position is part of the unique configuration of the hyomandibular apparatus in orangutans. Because the orangutan lacks a digastric muscle that can move the hyoid prior to (or during) mandibular depression, the primary jaw opening mechanism has been mechanically decoupled from that of hyoid movement. Inability to move the hyoid with the digastric muscle potentially results in differences in the recruitment of other hyoid muscles and in hyoid movement during mastication, food transport, and swallowing.
CONCLUSIONS

Functional differentiation in the anterior and posterior bellies of the digastric is documented here for the first time in a primate. The reason or reasons behind the loss of the anterior digastric in the orangutan remain to be determined.

This study has shown that the absence of the anterior digastric in the orangutan has several functional consequences. The orangutan has gained a mandibular insertion of the posterior digastric, and the posterolateral position of the insertion may be partly responsible for the marked transverse movements of the mandible during jaw opening. It is also possible that the mandibular insertion is advantageous for producing large opening moments, especially at wider gapes (cf. Weijs and Muhl, 1987). Besides having to use the geniohyoid as the primary protractor of the hyoid, the orangutan has lost the ability to elevate the hyoid apparatus and depress the mandible via contraction of a single muscle capable of effecting extensive mouth opening. By definition, decoupling of this mechanism alters the muscular forces acting on the hyoid apparatus and may signify a unique pattern of hyomandibular movements during mastication, food transport, and/or swallowing.

The functional consequences documented here need to be accounted for in hypotheses that explain the loss of the anterior digastric. Future research on this topic should focus on understanding what factors influence the relative positions of the jaws, pharynx, and hyoid in orangutans’ and include experimental research on the activity patterns of other hyoid muscles (e.g., the infrahyoid group, hyoglossus, stylohyoid, and the middle constrictor) and on the movements of the hyomandibular apparatus in nonhuman hominoids.

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