

Symphyseal Fusion and Jaw-Adductor Muscle Force: An EMG Study

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ABSTRACT The purpose of this study is to test various hypotheses about balancing-side jaw muscle recruitment patterns during mastication, with a major focus on testing the hypothesis that symphyseal fusion in anthropoids is due mainly to vertically- and/or transversely-directed jaw muscle forces. Furthermore, as the balancing-side deep masseter has been shown to play an important role in wishboning of the macaque mandibular symphysis, we test the hypothesis that primates possessing a highly mobile mandibular symphysis do not exhibit the balancing-side deep masseter firing pattern that causes wishboning of the anthropoid mandible. Finally, we also test the hypothesis that balancing-side muscle recruitment patterns are importantly related to allometric constraints associated with the evolution of increasing body size. Electromyographic (EMG) activity of the left and right superficial and deep masseters were recorded and analyzed in baboons, macaques, owl monkeys, and thick-tailed galagos. The masseter was chosen for analysis because in the frontal projection its superficial portion exerts force primarily in the vertical (dorsoventral) direction, whereas its deep portion has a relatively larger component of force in the transverse direction. The symphyseal fusion-muscle recruitment hypothesis predicts that unlike anthropoids, galagos develop bite force with relatively little contribution from their balancing-side jaw muscles. Thus, compared to galagos, anthropoids recruit a larger percentage of force from their balancing-side muscles. If true, this means that during forceful mastication, galagos should have working-side/balancing-side (W/B) EMG ratios that are relatively large, whereas anthropoids should have W/B ratios that are relatively small. The EMG data indicate that galagos do indeed have the largest average W/B ratios for both the superficial and deep masseters (2.2 and 4.4, respectively). Among the anthropoids, the average W/B ratios for the superficial and deep masseters are 1.9 and 1.0 for baboons, 1.4 and 1.0 for macaques, and both values are 1.4 for owl monkeys. Of these ratios, however, the only significant difference between thick-tailed galagos

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and anthropoids are those associated with the deep masseter. Furthermore, the analysis of masseter firing patterns indicates that whereas baboons, macaques and owl monkeys exhibit the deep masseter firing pattern associated with wishboning of the macaque mandibular symphysis, galagos do not exhibit this firing pattern. The allometric constraint-muscle recruitment hypothesis predicts that larger primates must recruit relatively larger amounts of balancing-side muscle force so as to develop equivalent amounts of bite force. Operationally this means that during forceful mastication, the W/B EMG ratios for the superficial and deep masseters should be negatively correlated with body size. Our analysis clearly refutes this hypothesis. As already noted, the average W/B ratios for both the superficial and deep masseter are largest in thick-tailed galagos, and not, as predicted by the allometric constraint hypothesis, in owl monkeys, an anthropoid whose body size is smaller than that of thick-tailed galagos. Our analysis also indicates that owl monkeys have W/B ratios that are small and more similar to those of the much larger-sized baboons and macaques. Thus, both the analysis of the W/B EMG ratios and the muscle firing pattern data support the hypothesis that symphyseal fusion and transversely-directed muscle force in anthropoids are functionally linked. This in turn supports the hypothesis that the evolution of symphyseal fusion in anthropoids is an adaptation to strengthen the symphysis so as to counter increased wishboning stress during forceful unilateral mastication. In contrast, the W/B EMG ratios provide no (or arguably weak) support for the hypothesis that symphyseal fusion and vertically-directed muscle force are functionally linked, and the data clearly refute the hypothesis that balancing-side jaw-muscle recruitment patterns are influenced by allometric factors associated with the evolution of increasing body size. *Am J Phys Anthropol* 112:469–492, 2000. © 2000 Wiley-Liss, Inc.

When mammals chew hard or tough foods, they typically do so unilaterally, i.e., food is mechanically reduced in size between their postcanine teeth on only one side of the jaw. When mammals chew unilaterally, they typically exhibit bilateral but differential recruitment of their jaw-adductor muscles, i.e., both the working-side (the chewing side) and the balancing-side (the nonchewing side) jaw muscles are activated asynchronously to produce various jaw movements and jaw muscle forces.

Recently we tested two hypotheses about how balancing-side jaw-adductor muscles are recruited in primates (Hylander et al., 1998). One of these, the *symphyseal fusion-muscle recruitment* hypothesis, states that increased balancing-side jaw-adductor muscle force is linked to the evolution of symphyseal fusion in anthropoid primates. That is, symphyseal fusion is an adaptation to strengthen the symphysis so as to prevent its structural failure due to increased stress

associated with increased recruitment of balancing-side muscle force during forceful mastication. In contrast, the *allometric constraint-muscle recruitment* hypothesis states that increased balancing-side muscle force is simply linked to allometric constraints on jaw-adductor muscle force production associated with the evolution of increasing body size. That is, larger primates must recruit relatively higher levels of balancing-side muscle force so as to generate equivalent amounts of bite force during forceful mastication.

These two hypotheses, which are not necessarily mutually exclusive, were tested by analyzing mandibular corpus bone-strain data recorded from long-tailed macaques, thick-tailed galagos, and owl monkeys, as these subjects engaged in forceful mastication (Hylander et al., 1998). The strain data indicate that for all species analyzed, peak working-side corpus strains are large and broadly similar in magnitude. Moreover, for

anthropoids the balancing-side strains are slightly smaller than their working-side strains, whereas for galagos the balancing-side strains are much smaller than their working-side strains. Furthermore, the balancing-side strains of anthropoids are much larger than the balancing-side strains of galagos. As balancing-side corpus strains are predominately the result of balancing-side muscle force (Hylander, 1977; Dechow and Carlson, 1983), these data indicate that compared to anthropoids, galagos recruit much less balancing-side muscle force during mastication.

Macaques and owl monkeys have a rigid fully-fused mandibular symphysis, which is the derived condition for extant anthropoids, whereas adult thick-tailed galagos have an unfused symphysis, which is a retention of the primitive mammalian condition. Furthermore, the symphysis of thick-tailed galagos is highly mobile and is not only structurally weaker than a fully-fused symphysis, but is structurally weaker than the unfused symphyses of most other extant primates (Beecher, 1977, 1979). Thus, the bone strain data in combination with the above morphological observations support the symphyseal fusion hypothesis, and the strain data alone appear to refute the allometric constraint hypothesis (Hylander et al., 1998).

Jaw muscle force, symphyseal stress and symphyseal fusion

If increased recruitment of balancing-side adductor muscle force in anthropoids is indeed linked to the evolution of symphyseal fusion, it has been hypothesized that this increased force is either vertically (dorsoventrally) directed, transversely (mediolaterally) directed, or is some near equal combination of these force components (cf. Hylander, 1985; Hylander et al., 1995, 1996, 1998; Ravosa, 1996; Ravosa and Hylander, 1994; Ravosa and Simons, 1994). If vertically directed, then a likely functional correlate of this increase in vertically-directed muscle force is a relative increase in vertically-directed bite force, i.e., an increase in crushing or vertical shearing forces along postcanine teeth. As an increase in vertically-directed muscle force is likely to cause

the symphysis to experience an increase in bending in the frontal plane (due to axial torsion of the mandibular corpora) and dorsoventral shear (Hylander, 1984), then perhaps symphyseal fusion is an adaptive response to prevent structural failure by more effectively resisting increased symphyseal stresses associated with these particular shearing and bending regimes.

If the increased jaw-adductor muscle force in anthropoids is primarily transversely directed, then a likely functional correlate of this force is a relative increase in transversely-directed bite force, i.e., a relative increase in grinding and/or transverse shearing forces along postcanine teeth. As an increase in transversely-directed balancing-side muscle force causes an increase in lateral transverse bending or wishboning of the symphysis (Hylander, 1984), then perhaps symphyseal fusion is an adaptive response to prevent structural failure by more effectively resisting increased symphyseal stresses associated with this particular bending regime.

Alternatively, perhaps the increased balancing-side muscle force is some near equal combination of both an increase in vertically- and transversely-directed muscle forces, and therefore perhaps symphyseal fusion is an adaptive response to more effectively resist increased stresses associated with an increase in some combination of all of the above loading regimes.

There exists little experimental data that deal directly with the evolution of symphyseal fusion, symphyseal stress, and the direction of jaw-adductor muscle force during chewing and biting in primates. With the exception of macaques, there are no *in vivo* symphyseal strain data, and with the exception of macaques, baboons, and humans, there are relatively little relevant data on jaw-muscle function during mastication. The symphyseal strain data indicate that although the macaque mandibular symphysis experiences varying degrees of dorsoventral shear and bending in the frontal plane, the highest levels of symphyseal stress during mastication are associated with wishboning (Hylander, 1984, 1985). Furthermore, analyses of muscle function indicate that for macaques the pronounced late ac-

tivity of the balancing-side deep masseter is largely responsible for the occurrence of symphyseal wishboning during mastication (Hylander and Johnson, 1994).

In spite of our apparent inability to determine what loading regimes are acting on the symphyses of galagos and owl monkeys, we can reasonably assume that force from their balancing-side jaw-adductor muscles have a vertical component which contributes to dorsoventral symphyseal shear stress and bending in the frontal plane (cf. Hylander, 1979a). What we do not know, however, is whether these loads are significantly different between owl monkeys and galagos, and whether or not these species possess the macaque type of muscle firing pattern that causes the macaque mandibular symphysis to experience wishboning during mastication.

Purpose of this study

The main purpose of this study is to test various hypotheses that link symphyseal fusion to jaw muscle recruitment patterns during mastication. Toward this end, we present a detailed electromyographic (EMG) analysis of the superficial and deep masseters of baboons, macaques, owl monkeys, and galagos. This analysis enables us to characterize activity patterns for, when viewed in the frontal projection, one portion of the jaw-adductor muscle mass that has a relatively larger vertical orientation, the superficial masseter, and one portion that has a relatively larger transverse orientation, the deep masseter (Hylander and Johnson, 1994). These pronounced differences in orientation for macaques and galagos can be seen in Figures 20 and 21 of Hylander (1979a). Dissection of these muscles in baboons and owl monkeys reveals a similar orientation simply because whereas the superficial and deep masseters both originate from the zygomatic arch, the superficial masseter inserts along the mandible well below the insertion site of the deep masseter. Thus, the deep masseter is always more transversely aligned (also cf. Antón, 1999; Gaspard et al., 1973; Schumacher, 1961). Dissection also reveals that the superficial masseter is about three times larger than that of the deep masseter. Finally, Antón's

study indicates that the physiological cross sectional area of the macaque superficial masseter is about twice as large as the deep masseter (Antón, 1993, 1999).

A detailed EMG analysis of these muscles will give us some insight as to whether there are major differences in muscle recruitment and firing patterns, and by inference, in symphyseal loading patterns, between anthropoids and thick-tailed galagos during mastication. Furthermore, as adult owl monkeys weigh approximately 1 kilogram (kg) and our baboons weigh between 16 kg and 23 kg, and the body weights of adult thick-tailed galagos (1.5 to 2 kg) and long-tailed macaques (4 to 7 kg) are distributed within this wide range of values, this analysis can also provide clues as to whether there are important differences in recruitment patterns that are linked to allometric constraints on jaw-adductor muscle force production.

Testing balancing-side muscle-recruitment hypotheses

Table 1 lists and numbers (from 1 to 7) a series of balancing-side muscle-recruitment hypotheses. This table also indicates the types of data that provide support for each of these hypotheses.

Hypothesis 1. In contrast to anthropoids, galagos may recruit relatively less overall balancing-side muscle force during the power stroke of mastication, i.e., bite force in galagos may be generated almost entirely by the recruitment of force from their working-side muscles. If so, as EMG activity of the masseter is highly correlated with relative masseter force during the power stroke of mastication in primates (Hylander and Johnson, 1989, 1993), compared to anthropoids, galagos are predicted to have a relatively large working-side/balancing-side (W/B) ratio of peak EMG values for both the superficial and deep masseter muscles. If true, this outcome would provide support for the hypothesis that increased vertically- and transversely-directed balancing-side muscle forces are linked to the evolution of symphyseal fusion in anthropoids.

TABLE 1. Testing balancing-side muscle-recruitment hypotheses

Number	Muscle-recruitment hypotheses	Working/balancing EMG ratios							
		Superficial masseter				Deep masseter			
		Baboons	Macaques	Owl monkeys	Galagos	Baboons	Macaques	Owl monkeys	Galagos
1	Symphyseal fusion: Vertical ¹ and transverse forces ²	Small	Small	Small	Large	Small	Small	Small	Large
2	Symphyseal fusion: Primarily transverse force	Near identical values or galago values overlap with anthropoid values				Small	Small	Small	Large
3	Symphyseal fusion: Primarily vertical force	Small	Small	Small	Large	Near identical values or galago values overlap with anthropoid values			
4	Allometric constraint	Small	Medium	Largest	Large	Small	Medium	Largest	Large
5	Allometric constraint and symphyseal fusion: Vertical and transverse forces	Small	Medium	Large	Largest	Small	Medium	Large	Largest
6	Allometric constraint and symphyseal fusion: Primarily transverse force	Small	Medium	Largest	Large	Small	Medium	Large	Largest
7	Allometric constraint and symphyseal fusion: Primarily vertical force	Small	Medium	Large	Largest	Small	Medium	Largest	Large

¹ Increased vertical muscle force causes the symphysis to experience increased bending stress due to axial torsion of the mandibular corpora and increased dorsoventral shear stress.

² Increased transverse muscle force causes the symphysis to experience increased wishboning.

Hypothesis 2. On the other hand, and similar to anthropoids, galagos may recruit a substantial amount of force from their balancing-side superficial masseter (cf. Hylander and Johnson, 1997), but unlike anthropoids, they may recruit relatively little force from their balancing-side deep masseter. If so, the data will demonstrate that both anthropoids and galagos have near identical or overlapping W/B EMG ratio values for the superficial masseter, but for the deep masseter anthropoids will have a small W/B ratio whereas galagos will have a large W/B ratio. This outcome would provide support for the hypothesis that the evolution of symphyseal fusion in anthropoid primates is linked to increased transversely-directed balancing-side muscle forces associated with the deep masseter.

Hypothesis 3. Another possibility, and again similar to anthropoids, galagos may recruit a substantial amount of force from their balancing-side deep masseter, but unlike anthropoids, they may recruit relatively little force from their balancing-side superficial masseter. If so, the data will demonstrate that both anthropoids and galagos have near identical or overlapping W/B ratios for the deep masseter, but for the superficial masseter anthropoids will have a small W/B ratio and galagos will have a large W/B ratio. This outcome would pro-

vide support for the hypothesis that the evolution of symphyseal fusion in anthropoid primates is linked to increased vertically-directed balancing-side muscle forces.

Hypothesis 4. But yet another possibility is that larger primates may recruit relatively high levels of balancing-side muscle force simply to generate equivalent amounts of bite force during mastication. If true, the data will indicate that the W/B EMG ratios for the superficial and deep masseter are negatively correlated with body size (Hylander et al., 1998). Baboons will have the smallest W/B ratios, owl monkeys the largest, and for galagos and macaques these ratios will be intermediate with the galagos having larger values than the macaques. If so, this outcome would provide support for hypothesis 4, and refute hypotheses 1, 2, and 3. Of course support for hypotheses 1, 2, or 3 constitutes a refutation of hypothesis 4 with the following exceptions.

Hypotheses 5, 6, and 7. The symphyseal fusion hypotheses (hypotheses 1, 2, or 3) are not necessarily mutually exclusive of the allometric constraint hypothesis (hypothesis 4). That is, although galagos may indeed have the largest W/B EMG ratios, supporting hypotheses 1, 2, or 3, the W/B EMG ratios of the superficial and/or deep masse-

ter for anthropoids may be negatively correlated with body size (hypotheses 5, 6, or 7, respectively).

Masseter firing patterns and wishboning. We also propose to determine for galagos and owl monkeys whether they exhibit the macaque and baboon pattern of the late peak activity in the balancing-side deep masseter because this firing pattern contributes to wishboning of the symphysis in macaques (and presumably baboons) (Hylander and Johnson, 1994). Most notably, this hypothesis predicts that the balancing-side deep masseter of anthropoids reaches peak activity well after peak activity of the balancing-side superficial masseter, at a time when vertically-directed muscle force is rapidly declining during the most terminal portion of the power stroke (cf. Hylander and Johnson, 1994). If it turns out that owl monkeys have this firing pattern and galagos do not, this would provide support for the hypothesis that the evolution of symphyseal fusion in anthropoids is linked to transversely-directed muscle forces (cf. *Hypothesis 2*).

MATERIALS AND METHODS

Subjects

The following five baboons, four macaques, two owl monkeys, and three galagos served as subjects: five *Papio anubis* consisting of one adult female (baboon 1), two adult males (baboons 2 and 3), and two subadult males (baboons 4 and 5); three *Macaca fascicularis* consisting of two adult females (macaques 2 and 5) and one adult male (macaque 7); one *Macaca fuscata* adult male (macaque 11); two *Aotus trivirgatus* consisting of one adult female (owl monkey 2) and one adult male (owl monkey 1); and finally two *Otolemur crassicaudatus* adult males (galagos 6 and 7) and one *Otolemur garnettii* adult male (galago 8). Prior to the experiments all subjects were trained to eat various foods in the laboratory. All subjects were used for at least two and as many as six separate experiments. These different experiments are indicated in our tables by letters, e.g., macaque 2, Exp. A.

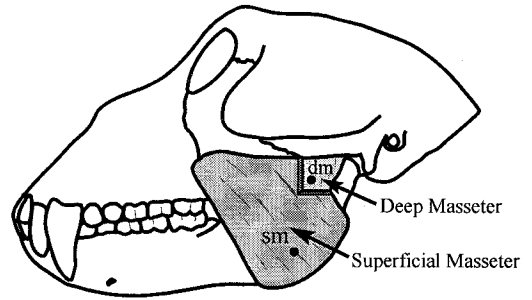


Fig. 1. Drawing of the lateral view of a macaque skull and the superficial and deep portions of the masseter muscle. The solid black dots indicate the location of the bipolar fine-wire electrodes in the deep (dm) and superficial (sm) portions of the masseter.

EMG electrodes and electrode placement procedure

Fine-wire indwelling bipolar electrodes were placed within the left and right middle portion of the superficial and deep masseter muscles (Fig. 1). In all instances, the tips of the electrodes were first placed into a 25-gauge needle, and the needle was then inserted into one of the above muscles until its point encountered mandibular bone. The needle was then withdrawn leaving the electrode tips embedded in muscle about 3–5 mm from the surface of the mandible. The electrodes in the superficial masseter were positioned midway between its anterior and posterior borders, about 5–10 mm above the lower border of the angle of the mandible (Fig. 1). The electrode tips in the deep masseter were positioned 5–10 mm below the lower border of the zygomatic arch. In order to reach the deep masseter, the needle was inserted immediately below the zygomatic arch at a 45° angle relative to both the transverse and coronal planes. Except for the baboons, the needle was inserted near the junction of the middle and posterior thirds of the zygomatic arch. For baboons it was inserted near the junction of the anterior and middle thirds of the arch because dissections revealed a more rostral position for this muscle. All electrodes were inserted with the subjects under light sedation using a combination of acepromazine and ketamine (Connolly and Quimby, 1978). The electrodes and the overall placement procedures are described in detail elsewhere

(Hylander and Johnson, 1985). As the subjects were not killed, electrode position was not verified by dissection.

Recording procedure

Prior to recovery from the sedative, the subject was placed in a restraining chair (baboons and macaques) or restraining sling-suit (galagos and owl monkeys) especially designed to permit normal head, neck, and jaw movements during mastication. Once the animal fully recovered from sedation, it was fed pieces of apple skin and hard and/or tough foods, i.e., unpopped popcorn kernels, dried gelatin candy (dried gummy bears), and dried apricots and prunes. The EMG potentials were simultaneously amplified and filtered (bandpass 100–3,000 Hz) and then recorded with a 14-channel FM tape recorder at 15 inches/second. Details of the recording procedure are the same as described previously (Hylander and Johnson, 1989, 1994). The data presented here are based on 46 separate experiments (16 baboon, 10 macaque, 8 galago and 12 owl monkey experiments).

All EMG data were recorded as subjects vigorously chewed various food items. At this time we identified whether the subject chewed on the left or right sides by carefully observing during the opening stroke of mastication whether the subject's tongue positioned the food on the left or right side of the mouth. As is well known, food positioning during jaw opening determines the chewing side for the next power stroke. The location of the chewing side was recorded on an audio channel of the tape recorder. We continued to feed the various foods in an intermittent fashion and data were recorded until either we obtained a surplus of data or the animal refused to eat any additional food. At the conclusion of the recording session the animal was sedated, the electrodes were removed, and the animal was returned to its cage. Recovery from the procedure was uneventful in all subjects.

EMG quantification

All EMG recordings of each chewing sequence were initially reproduced for visual examination by playing the raw EMG data from the tape recorder into two multiple-

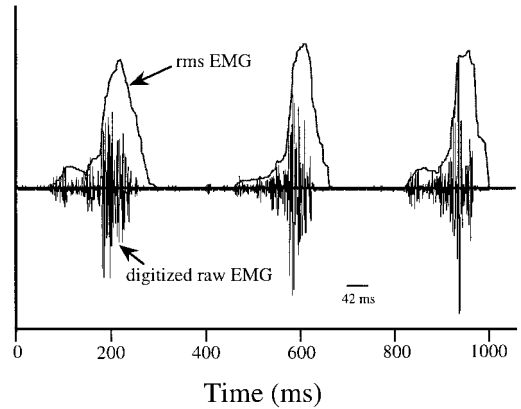


Fig. 2. Digitized raw EMGs and the corresponding root-mean-square (rms) EMGs for the working-side superficial masseter of a male macaque during mastication of popcorn kernels. Time is in milliseconds (ms). The rms values were calculated using a 42 ms time constant for reasons outlined in Hylander and Johnson (1993). The use of this time constant results in a EMG waveform that approximates the waveform of jaw muscle force. Each rms EMG value represents the root-mean-square of the raw digitized EMG values for the previous 42 ms. This results in a latency period between the apparent "peak" raw EMG and the actual peak rms EMG value. Moreover, the rms EMG value reaches zero 42 ms after the raw EMG appears to reach zero. There is also a latency period between peak rms EMG and peak muscle force. On average, peak muscle force follows peak rms EMG by about 30 ms (Hylander and Johnson, 1993).

channel dual beam storage oscilloscopes. As macaques and baboons rarely shift chewing sides during a chewing sequence, we selected for analysis one sequence of chewing on the left and one for chewing on the right, for each food. In contrast, owl monkeys and galagos usually shift chewing sides after every 3 or 4 chewing cycles. Therefore, we selected for analysis, one sequence that started with chewing on the left and one that started with chewing on the right.

For each chewing sequence analyzed the EMG data were played from the FM tape recorder into a 16-channel analog-to-digital converter (12-bit resolution), and the digitized values were written to the hard disk of a microcomputer. Each channel was sampled and digitized at a rate of 10,000 Hz with a channel separation time of 6.25 microseconds (msec). The digitized values were then read back into the microcomputer for subsequent processing and analysis.

The digitized raw EMG values (Fig. 2)

were first filtered with a digital Butterworth band-pass filter (100–3000 Hz). We then quantified the EMG by calculating the root-mean-square (rms) values from the raw digitized values employing a 42 millisecond (ms) time constant (Fig. 2) (Hylander and Johnson, 1993). The rms values were calculated in 2 ms intervals for the entire chewing sequence. We then identified the largest rms value for each electrode throughout a given experiment, regardless as to whether it was a working- or balancing-side muscle. For each power stroke the peak values for each electrode were then scaled by assigning a value of 1.0 to the largest value, and the remaining smaller peak values were scaled in a linear fashion. Thus, for each power stroke and muscle there is a scaled value for peak EMG activity.

W/B EMG ratios

For each power stroke the scaled peak working-side EMG value was then divided by the scaled peak balancing-side EMG value. We refer to this value as the working/balancing (W/B) EMG ratio. If the working-side EMG level is larger than the balancing-side level, the W/B ratio is larger than 1.0. Conversely, if the balancing-side EMG level is larger, the W/B ratio is less than 1.0. As noted in the results, in the majority of instances the working-side EMG values tend to be larger than the balancing-side values. Activity of the deep masseter in macaques and baboons are a notable exception to this pattern.

As the W/B EMG ratio is a derived variable with values distributed above and below 1.0 and with a distribution that is skewed to the right, the mean of these ratios may not be a good estimate of central tendency (Hylander and Johnson, 1994). For example, if during the power stroke of chewing the peak scaled working-side deep masseter is 50% larger than is the peak scaled balancing-side deep masseter, the W/B ratio for that power stroke is 1.5. If during the next power stroke the opposite condition prevails, the W/B ratio is 0.67. The mean of these two W/B values is 1.08, erroneously suggesting that on average the peak working-side deep masseter is larger than is the peak balancing-side deep masseter, when in

fact for these two power strokes these muscles exhibit equal peak activity. In order to eliminate this problem, a log transformation of the data was necessary so as to normalize the distribution of W/B values (Sokal and Rohlf, 1981). After determining mean W/B values of the log transformed data, the mean values were then transformed back to their original scale. Means (and standard deviations) were determined for the W/B EMG ratios for each experiment and subject. Grand means of the W/B EMG ratio were calculated for each group of primates based on experiment mean values.

Due to inherent problems associated with the statistical testing of ratios, we intend to focus the analysis on the grand means, subject means, and experiment means of these ratios. Our main goal for this portion of the analysis is to determine if the W/B ratios of the superficial and/or deep masseter in galagos *consistently* differ from those of anthropoids.

Jaw muscle firing patterns

So as to establish a standard uniform procedure for the analysis of muscle firing patterns, the timing of peak EMG activity of the working- and balancing-side deep masseters and the balancing-side superficial masseter were compared to the peak EMG activity of our reference muscle, the working-side superficial masseter. Furthermore, the peak timing differences were also determined between (1) the working- and balancing-side deep masseters, (2) the balancing-side superficial and deep masseters, and (3) the working-side deep and balancing-side superficial masseters. In addition to determining the timing differences between peak EMG values, the timing differences between 25%, 50% and 75% level of peak EMG values were also determined for each power stroke during loading and unloading.

The main goal for this portion of the analysis is to determine whether only the anthropoids possess the masseter firing pattern thought to be associated with wishboning of the macaque symphysis (Hylander et al., 1987). The macaque firing pattern is characterized by peak activity of the working-side deep and balancing-side superficial masseters *preceding* peak activity

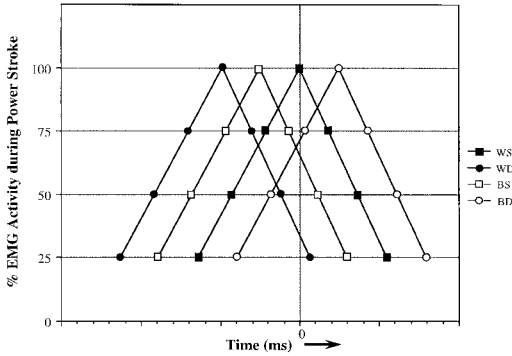


Fig. 3. Predictions of masseter firing pattern associated with wishboning of the symphysis. The working hypothesis predicts the occurrence of this pattern in only those primates with a fully fused mandibular symphysis, i.e., in extant anthropoids, but not in those prosimians with a highly mobile mandibular symphysis, such as thick-tailed galagos. The working-side deep masseter peaks first and the balancing-side deep masseter peaks last. Furthermore, the balancing-side superficial masseter peaks after the working-side deep and before the working-side superficial masseter. The vertical line indicates peak activity in the reference muscle, the working-side superficial masseter. Symbols: solid squares and circles, working-side superficial and deep masseter, respectively; open squares and circles, balancing-side superficial and deep masseter, respectively. Abbreviations: WS, working-side superficial masseter; WD, working-side deep masseter; BS, balancing-side superficial masseter; BD, balancing-side deep masseter.

of the working-side superficial masseter, and most importantly, by peak activity of the balancing-side deep masseter *following* peak activity of the working-side superficial masseter (Hylander and Johnson, 1994) (Figs. 3 and 4). Thus, as noted earlier, this firing pattern results in the balancing-side deep masseter reaching peak force well after peak force of the balancing-side superficial masseter, at a time when overall vertically-directed jaw-adductor muscle force is rapidly declining during the terminal portion of the power stroke.

Means and standard deviations were calculated for all timing values for each individual experiment and each subject. Grand means and mean standard deviations were then calculated from the mean values for each experiment. Unless indicated, all tests of significance are of the grand means. As our EMG timing data may not satisfy all of the requirements for parametric statistical tests, the mean timing differences in peak

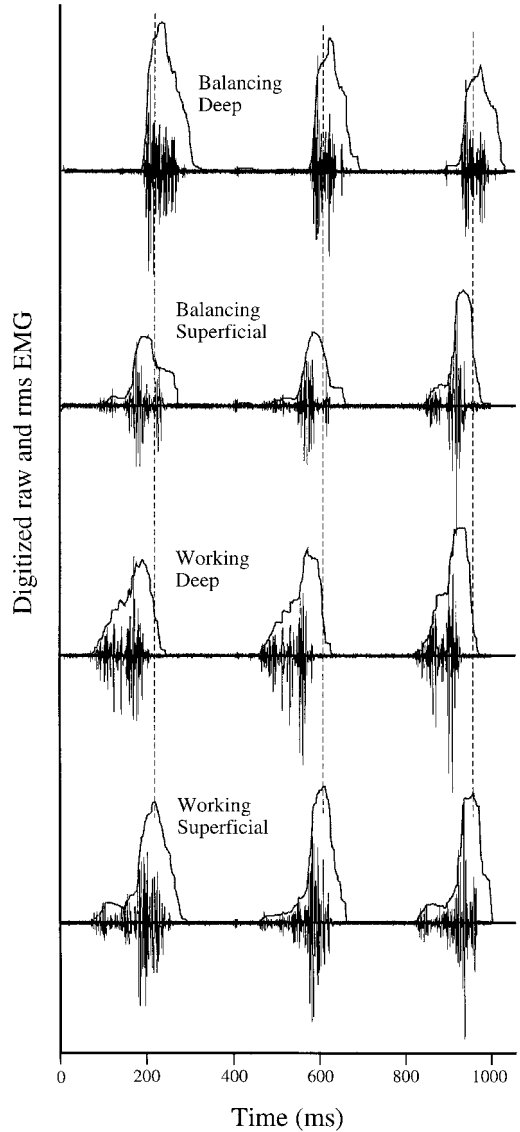


Fig. 4. Digitized raw and rms EMGs of the working- and balancing-side deep and superficial masseters in a male macaque during mastication of popcorn kernels. On average the working-side deep masseter is the first muscle to reach peak activity, and the balancing-side deep masseter is the last to reach peak activity. Moreover, peak activity in the balancing-side superficial masseter precedes peak activity in the working-side superficial masseter. The dashed vertical lines indicate peak activity in the reference muscle, the working-side superficial masseter.

EMGs between muscles were tested for significance at the .05 level by using a non-parametric test, the Wilcoxon signed-ranks

test for paired comparisons. When peak EMG of a muscle was predicted to either precede or follow peak EMG of another muscle a one-tailed test of significance was utilized; otherwise, all tests of significance were two-tailed tests.

Data selection

Earlier work has established that among macaques W/B masseter muscle force ratios are generally influenced by overall masticatory force levels, and that the lowest W/B ratios (which are close to 1.0) are usually associated with the more forceful power strokes, i.e., during the chewing of hard and/or tough foods (Hylander et al., 1992; Hylander and Johnson, 1997). Furthermore, biomechanical adaptations in the craniofacial region are likely to be in response to the more intense forceful loading regimes. Therefore, we will mainly present data recorded during the chewing of hard or tough foods. For each experiment, we will also analyze W/B ratios for 10 of the largest peak EMG values during the chewing of hard or tough foods so as to restrict further the analysis to the most forceful power strokes. The identification of these power strokes was operationalized by selecting those power strokes with the five largest balancing-side superficial masseter EMG values for chewing on the left and the five largest values for chewing on the right.

RESULTS

Typically, some subjects refused to eat certain foods. All, however, chewed at least one of the hard or tough foods on both left and right sides. Therefore, EMG data were recorded from all subjects during episodes of relatively forceful and vigorous mastication. Among galagos, the balancing-side EMGs were often very low in magnitude even though their working-side values were consistently large. When this occurs this causes the W/B ratio to become very large, and in theory the W/B EMG ratio can approach infinity. In order to prevent a few unusually large ratio values from grossly distorting the overall mean W/B ratios, we employed a cutoff value of 10 for each individual ratio. Thus, any W/B ratios larger than 10 were simply assigned a value of 10.0. We were

concerned that if this procedure was not employed, we might erroneously conclude that galagos routinely recruit relatively little balancing-side muscle force when in fact their mean W/B ratios were overly influenced by one or two unusually large values.

We also found that frequently, at the very beginning of a chewing sequence, our subjects engaged in two or three prolonged and near isometric bites interrupted by extensive intraoral manipulation of the food item. Immediately following these behaviors, they then engaged in rhythmic chewing behaviors. Our W/B ratio and timing data are based entirely on these later rhythmic chewing behaviors.

W/B EMG ratios

Tables 2–5 present the descriptive statistics of the W/B ratios for sequences of chewing hard or tough foods. These tables also indicate mean values of the W/B ratios associated with the ten most forceful power strokes from these chewing sequences (in parentheses). Note that there are three different types of mean values in these tables: experiment means, subject means, and grand means. Table 6 consists of summary data of the grand mean values of the W/B masseter ratios.

Superficial masseter. The anthropoid W/B ratios of the superficial masseter for both the complete chewing sequences and the 10 most forceful power strokes are smaller than the W/B ratios for galagos. For the complete chewing sequences, the grand mean W/B ratios of baboons, macaques, owl monkeys, and galagos are 1.9, 1.4, 1.4, and 2.2, respectively. There is, however, considerable overlap of the experiment mean values between the anthropoids and galagos. For example, the individual experiment mean values for anthropoids range from 1.1 to 2.7, whereas for thick-tailed galagos these values range from 1.5 to 2.8. For the ten most forceful power strokes, there is a reduction in the grand mean values of baboons, macaques, owl monkeys, and galagos to 1.6, 1.0, 1.1, and 2.0, respectively. Similarly, there is still a considerable amount of overlap in the experiment mean values be-

TABLE 2. Descriptive statistics of baboon W/B EMG ratios for the superficial and deep masseter muscles during mastication of popcorn kernels¹

Subject	N	Superficial masseter			Deep masseter		
		Mean	(Mean)	SD	Mean	(Mean)	SD
Baboon 1							
Exp. A	58	2.7	(2.1)	1.58	1.1	(0.9)	0.17
Exp. C	79	1.7	(1.3)	0.73	1.2	(1.0)	0.35
Exp. D	47	1.3	(1.2)	0.24			
Exp. E	46	1.5	(1.4)	0.35			
Subject mean		1.8	(1.5)	0.73	1.2	(1.0)	0.26
Baboon 2							
Exp. A	103	2.3	(2.1)	0.73	1.1	(1.0)	0.17
Exp. B	64	2.0	(1.4)	1.23	0.8	(0.6)	0.29
Subject mean		2.2	(1.8)	0.98	1.0	(0.8)	0.23
Baboon 3							
Exp. A	72	1.7	(1.3)	0.42	1.3	(1.0)	0.29
Exp. B	40	1.8	(1.8)	0.37	1.0	(0.8)	0.20
Exp. C	57	1.7	(1.4)	0.44			
Exp. D	64	1.9	(1.7)	0.40			
Subject mean		1.8	(1.6)	0.41	1.1	(0.9)	0.25
Baboon 4							
Exp. A	70	1.7	(1.4)	0.25	0.7	(0.6)	0.23
Exp. B	58	1.8	(1.4)	0.36	0.8	(0.7)	0.16
Exp. C	55				0.9	(0.7)	0.29
Subject mean		1.8	(1.4)	0.31	0.8	(0.7)	0.23
Baboon 5							
Exp. A	63	2.5	(2.3)	0.45	0.9	(0.8)	0.19
Exp. B	81	2.1	(1.4)	0.73	1.2	(1.0)	0.29
Exp. C	75	2.5	(1.5)	1.12	1.4	(1.2)	0.40
Subject mean		2.4	(1.7)	0.77	1.2	(1.0)	0.29
Grand mean		1.9	(1.6)	0.63	1.0	(0.9)	0.25

¹ Mean values in parentheses (Mean) indicate mean W/B ratio for the 10 largest power stroke: (5 largest for both left and right side chews). N is number of power strokes; SD is standard deviation.

tween anthropoids and galagos (0.9 to 2.3 and 1.3 to 2.4, respectively).

Deep masseter. The anthropoid W/B ratios of the deep masseter for both the chewing sequences, and the ten most forceful power strokes are quite unlike the W/B ratios for galagos. For the chewing sequences the W/B deep masseter ratios for baboons, macaques, owl monkeys, and galagos are 1.0, 1.0, 1.4, and 4.4, respectively. For anthropoids, the mean W/B ratios for each experiment range from 0.7 to 1.5, whereas for the galagos these values range from 2.1 to 9.5. Thus, of the 23 anthropoid and 8 galago experiments, there is *no overlap* whatsoever in the experiment mean values. Similar to the superficial masseter data, the average deep masseter W/B ratios of the ten most forceful power strokes decrease in size to 0.9, 0.8, 1.2, and 3.7 for baboons, macaques, owl monkeys, and galagos, respectively. Again there is no overlap in the range of

experiment mean values between anthropoids and galagos (0.6 to 1.2 and 1.9 to 10.0, respectively). Finally, as a cutoff value of 10 was imposed on the W/B ratios, and only galagos had values exceeding 10, we have underestimated the average W/B values for galagos, and therefore have underestimated the average differences of the deep masseter W/B ratios between the galagos and anthropoids.

Percent EMG activity of the masseter

Figure 5 is a bar graph representing percent EMG values for the working- and balancing-side masseters during the chewing of hard or tough foods and apple skin. (Recall that the galagos did not eat apple skin.) In addition to indicating some of what has already been described for the W/B ratios, this figure importantly demonstrates that on average all primate subjects recruit about the same percentage of peak EMG

TABLE 3. Descriptive statistics of macaque W/B EMG ratios for the superficial and deep masseter muscles during mastication of popcorn kernels¹

Subject	N	Superficial masseter			Deep masseter		
		Mean	(Mean)	SD	Mean	(Mean)	SD
Macaque 2							
Exp. A	41				0.9	(0.8)	0.18
Exp. B	38	1.3	(1.0)	0.39	0.7	(0.6)	0.44
Subject mean		1.3	(1.0)	0.39	0.8	(0.7)	0.31
Macaque 5							
Exp. B	61	1.3	(0.9)	0.41	1.1	(0.9)	0.22
Exp. C	68	1.2	(0.9)	0.40	1.3	(1.0)	0.20
Exp. D	92	1.2	(0.9)	0.32			
Subject mean		1.2	(0.9)	0.38	1.2	(1.0)	0.21
Macaque 7							
Exp. A	86	1.2	(1.0)	0.34	1.1	(1.0)	0.15
Exp. B	76	1.7	(1.2)	0.40			
Subject mean		1.5	(1.1)	0.37	1.1	(1.0)	0.15
Macaque 11							
Exp. A	83	1.8	(1.2)	0.70	0.9	(0.7)	0.24
Exp. B	103	1.6	(1.2)	0.44	0.9	(0.8)	0.18
Subject mean		1.7	(1.2)	0.57	0.9	(0.8)	0.21
Grand mean		1.4	(1.0)	0.43	1.0	(0.8)	0.23

¹ Mean values in parentheses (mean) indicate mean W/B ratio for the ten largest power strokes (five largest for both left and right side chews). N is number of power strokes; SD is standard deviation.

TABLE 4. Descriptive statistics of owl monkey W/B EMG ratios for the superficial and deep masseter muscles during mastication of hard or tough foods¹

Subject	Food	N	Superficial masseter			Deep masseter		
			Mean	(Mean)	SD	Mean	(Mean)	SD
Owl monkey 1								
Exp. A	Gummy bear	49	1.3	(1.1)	(0.36)	1.5	(1.2)	(0.64)
Exp. B	Gummy bear	34	1.4	(1.1)	(0.37)	1.2	(1.1)	(0.21)
Exp. C	Gummy bear	39	1.2	(1.0)	(0.35)			
Exp. D	Hard apricot	39	1.3	(1.1)	(0.41)			
Exp. E	Hard prune	56	1.3	(1.0)	(0.28)			
Exp. F	Hard prune	21	1.7	(1.2)	(1.05)			
Subject mean			1.4	(1.1)	(0.47)	1.4	(1.2)	(0.43)
Owl monkey 2								
Exp. A	Gummy bear	42	1.3	(1.1)	(0.24)	1.3	(1.1)	(0.24)
Exp. B	Hard apricot	30	1.5	(1.3)	(0.44)	1.4	(1.2)	(0.43)
Exp. C	Hard prune	42	1.1	(1.0)	(0.20)			
Exp. D	Hard prune	47	1.8	(1.2)	(0.80)			
Exp. E	Hard prune	69	1.1	(1.0)	(0.19)			
Exp. F	Hard prune	75	1.4	(1.1)	(0.49)			
Subject mean			1.4	(1.1)	(0.39)	1.4	(1.2)	(0.34)
Grand mean			1.4	(1.1)	(0.43)	1.4	(1.2)	(0.38)

¹ Mean values in parentheses (mean) indicate mean W/B ratio for the ten largest power strokes (five largest for both left and right side chews). N is number of power strokes; SD is standard deviation.

activity of their working-side muscles during the chewing of hard or tough foods (from 65% to 75% for the working-side superficial and deep masseters). In contrast, the balancing-side muscles are more variable. For the balancing-side superficial masseter the values range from 35% (baboons and galagos) to 57% (owl monkeys), with macaques

somewhat intermediate at 51%. The largest range in percentage values, however, is associated with the balancing-side deep masseter. Although anthropoids recruit on average from 58% (owl monkeys) to 65% and 66% (baboons and macaques) of peak EMG activity, galagos only recruit about 25% of peak activity of the balancing-side deep masseter.

TABLE 5. Descriptive statistics of galago W/B EMG ratios for the superficial and deep masseter muscles during mastication of hard or tough foods¹

Subject	Food	N	Superficial masseter			Deep masseter		
			Mean	(Mean)	SD	Mean	(Mean)	SD
Galago 6								
Exp. A	Gummy bear	40	2.1	(1.7)	0.67	6.0	(4.4)	1.72
Exp. B	Gummy bear	29	2.4	(2.3)	0.66	9.5	(10.0)	1.61
Exp. C	Hard apricot	37	1.5	(1.3)	0.47	4.5	(3.3)	0.50
Subject mean			2.0	(1.8)	0.60	6.7	(5.9)	1.28
Galago 7								
Exp. A	Hard prune	29	2.6	(2.1)	1.22	3.0	(2.6)	0.98
Exp. B	Gummy bear	71	2.6	(2.4)	0.73	2.8	(1.9)	0.91
Exp. C	Hard prune	29	2.8	(2.3)	1.26	3.5	(3.4)	0.69
Subject mean			2.7	(2.3)	1.07	3.1	(2.6)	0.86
Galago 8								
Exp. A	Hard apricot	28				3.6	(2.3)	1.89
Exp. B	Hard prune	19	1.7	(1.6)	0.53	2.1	(1.9)	0.51
Subject mean			1.7	(1.6)	0.53	2.9	(2.1)	1.20
Grand mean			2.2	(2.0)	0.79	4.4	(3.7)	1.10

¹ Mean values in parentheses (mean) indicate mean W/B ratio for the ten largest power strokes (five largest for both left and right side chews). N is number of power strokes; SD is standard deviation.

TABLE 6. Summary data of mean W/B ratios¹

Subject	Superficial masseter		Deep masseter	
	Overall	10 Largest	Overall	10 Largest
Baboon	1.9	1.6	1.0	0.9
Macaque	1.4	1.0	1.0	0.8
Owl Monkey	1.4	1.1	1.4	1.2
Galago	2.2	2.0	4.4	3.7

¹ Overall mean values are based on all power strokes within a chewing sequence. The ten largest mean values are based on the five largest power strokes for chewing on the left side and the five largest power strokes for chewing on the right side.

Compared to EMG values during the chewing of hard and tough foods, during apple skin chewing both macaques and baboons experience a reduction in activity of the working-side superficial masseter from approximately 65% to 45%, whereas the working-side deep masseter of macaques and baboons continues to exhibit about 65% of peak EMG activity. For owl monkeys, the reduction in EMG activity of the working-side superficial masseter is less and comparable to the reduction in activity of the working-side deep masseter. Overall the balancing-side muscles exhibit a pronounced reduction in EMG activity, particularly the deep masseter.

Masseter firing patterns of peak EMG

Tables 7–10 present the descriptive statistics for the firing patterns of the working- and balancing-side masseters during the

chewing of hard or tough foods. Each table indicates the mean timing differences in milliseconds of peak EMG activity of the working-side deep, the balancing-side superficial, and the balancing-side deep masseters, relative to peak EMG activity of the reference muscle, the working-side superficial masseter. Moreover, similar to the analysis of W/B ratios, there are three different types of mean values in these tables: experiment means, subject means, and grand means.

Positive values indicate that peak EMG of the muscle precedes peak activity of the reference muscle, and negative values indicate the reverse. Table 11 consists of summary data for the grand mean values presented in Tables 7–10. Table 12 consists of the grand means of three additional timing variables which characterize masseter firing patterns for these four groups of primates. These variables are the time intervals between peak EMG of (1) the working- and balancing-side deep masseters, (2) the working-side deep and the balancing-side superficial masseters, and (3) the balancing-side superficial and deep masseters.

Figures 6–9 indicate the mean timing differences of the working- and balancing-side masseter muscles throughout the power stroke for one baboon, macaque, owl monkey and galago subject. In addition to indi-

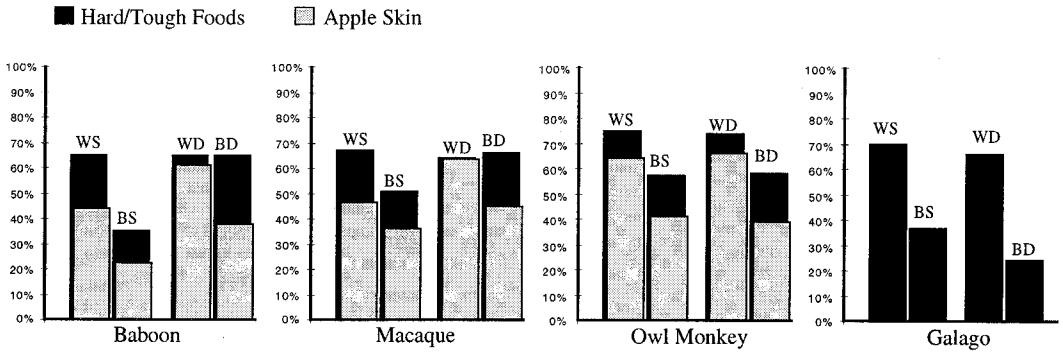


Fig. 5. Bar graphs of average percent EMG activity for all primates during the chewing of hard and/or tough foods and during the chewing of apple skin. Abbreviations: WS, working-side superficial; BS, balancing-side superficial; WD, working-side deep; BD, balancing-side deep masseters.

TABLE 7. Baboon timing differences (in milliseconds) between peak EMG activity of the balancing-side superficial masseter and working- and balancing-side deep masseters relative to the reference muscle, the working-side superficial masseter¹

Subject and food	N	Working deep		Balancing superficial		Balancing deep	
		Mean	SD	Mean	SD	Mean	SD
Baboon 1							
Exp. A Popcorn kernels	58	77	22.5	57	25.9	14	18.0
Exp. C Popcorn kernels	79	53	23.3	25	28.7	-5	22.9
Subject mean		65	22.9	41	27.3	5	20.5
Baboon 2							
Exp. A Popcorn kernels	103	53	20.3	16	18.1	-2	13.4
Exp. B Popcorn kernels	64	56	22.3	13	25.2	-6	15.2
Subject mean		55	21.3	15	21.7	-4	14.3
Baboon 3							
Exp. A Popcorn kernels	72	23	19.1	4	22.3	-11	21.1
Exp. B Popcorn kernels	40	37	17.1	22	21.5	4	17.7
Exp. C Popcorn kernels	57	59	22.9	3	31.8	0	19.3
Exp. D Popcorn kernels	64			4	25.4		
Subject mean		40	19.7	8	25.3	-2	19.4
Baboon 4							
Exp. A Popcorn kernels	70	49	25.0	19	21.2	-13	13.9
Exp. B Popcorn kernels	58	52	20.4	16	25.3	-6	21.8
Exp. C Popcorn kernels	27	55	21.1			-23	24.3
Subject mean		52	22.2	18	23.3	-14	20.0
Baboon 5							
Exp. A Popcorn kernels	63	46	13.7	15	15.2	-6	12.1
Exp. B Popcorn kernels	81	30	17.2	5	15.6	-15	11.9
Exp. C Popcorn kernels	75	14	18.6	16	17.2	-3	15.0
Subject mean		30	16.5	12	16.0	-8	13.0
Grand mean		47 ³	20.3	17 ³	22.6	-6 ²	17.4

¹ Positive values indicate that peak EMG activity of the muscle precedes peak EMG activity of the working-side superficial masseter. Negative values indicate the reverse condition. N is number of power strokes; SD is standard deviation.

² Grand mean value indicates that peak EMG activity of the balancing-side deep masseter follows peak EMG activity of the reference muscle ($P \leq .05$).

³ Grand mean values indicate that the peak EMG activity of the working-side deep masseter and balancing-side superficial masseter precede peak EMG activity of the reference muscle ($P \leq .001$).

cating the relative timing of peak EMG values, these figures also indicate the relative timing of 25%, 50%, and 75% of peak EMGs during loading and unloading.

Baboons and macaques. The overall firing patterns for baboons and macaques are remarkably similar, and therefore will be treated together. The mean timing differ-

TABLE 8. Macaque timing differences (in milliseconds) between peak EMG activity of the balancing-side superficial masseter and working- and balancing-side deep masseters relative to the reference muscle, the working-side superficial masseter¹

Subject and food	N	Working deep		Balancing superficial		Balancing deep	
		Mean	SD	Mean	SD	Mean	SD
Macaque 2							
Exp. A Popcorn kernels	20	82	24.3			5	23.0
Exp. B Popcorn kernels	38	81	34.5	34	25.1	-20	20.4
Subject mean		82	29.4	34	25.1	-8	21.7
Macaque 5							
Exp. B Popcorn kernels	61	71	29.7	25	26.0	-40	28.4
Exp. C Popcorn kernels	68	62	25.2	15	23.5	-40	26.7
Exp. D Popcorn kernels	92	68	22.7	13	20.3		
Subject mean		67	25.9	18	23.3	-40	27.6
Macaque 7							
Exp. A Popcorn kernels	86	74	27.0	16	28.9	-5	29.2
Exp. B Popcorn kernels	76			14	32.1		
Subject mean		74	27.0	15	30.5	-5	29.2
Macaque 11							
Exp. A Popcorn kernels	83	37	17.4	7	18.7	-26	13.4
Exp. B Popcorn kernels	103	41	16.7	13	20.5	-15	13.3
Subject mean		39	17.1	10	19.6	-21	13.4
Grand mean		65 ³	24.7	17 ³	24.4	-20 ²	22.1

¹ Positive values indicate that peak EMG activity of the muscle precedes peak EMG activity of the working-side superficial masseter. Negative values indicate the reverse condition. N is number of power strokes; SD is standard deviation.

² Grand mean value indicates that peak EMG activity of the balancing-side deep masseter follows peak EMG activity of the reference muscle ($P \leq .05$).

³ Grand mean values indicate that the peak EMG activity of the working-side deep masseter and balancing-side superficial masseter precede peak EMG activity of the reference muscle ($P \leq .01$).

TABLE 9. Owl monkey timing differences (in milliseconds) between peak EMG activity of the balancing-side superficial masseter and working- and balancing-side deep masseters relative to the reference muscle, the working-side superficial masseter¹

Subject and food	N	Working deep		Balancing superficial		Balancing deep	
		Mean	SD	Mean	SD	Mean	SD
Owl Monkey 1							
Exp. A Gelatin candy	49	4	17.0	-8	14.1	-22	13.2
Exp. B Gelatin candy	34	30	15.8	5	14.9	-7	16.3
Exp. C Gelatin candy	39			-5	10.8		
Exp. D Hard apricot	39			-11	36.2		
Exp. E Hard prune	56			-29	33.9		
Exp. F Hard prune	21			4	19.3		
Subject mean		17	16.4	-7	21.5	-15	14.8
Owl Monkey 2							
Exp. A Gelatin candy	42	11	5.8	6	5.9	-13	6.5
Exp. B Hard apricot	30	7	7.4	10	8.8	-1	7.1
Exp. C Hard prune	42			5	9.2		
Exp. D Hard prune	47			12	15.6		
Exp. E Hard prune	69			-3	7.8		
Exp. F Hard prune	75			6	10.0		
Subject mean		9	6.6	6	9.6	-7	6.8
Grand mean		13 ²	11.5	-1	15.5	-11 ²	10.8

¹ Positive values indicate that peak EMG activity of the muscle precedes peak EMG activity of the working-side superficial masseter. Negative values indicate the reverse condition. N is number of power strokes; SD is standard deviation.

² Grand mean values indicate that the peak EMG activity of the working-side deep masseter precedes and the balancing-side deep masseter follows peak EMG activity of the reference muscle ($P \leq .05$).

ences for 14 separate experiments on 5 different baboon subjects are presented in Table 7. The mean timing differences for nine

separate experiments on four different macaque subjects are presented in Table 8. The data indicate that on average peak EMG of

TABLE 10. Galago timing differences (in milliseconds) between peak EMG activity of the balancing-side superficial masseter and working- and balancing-side deep masseters relative to the reference muscle, the working-side superficial masseter¹

Subject and food	N	Working deep		Balancing superficial		Balancing deep	
		Mean	SD	Mean	SD	Mean	SD
Galago 6							
Exp. A Gelatin candy	40	12	22.6	28	27.9	11	17.2
Exp. B Gelatin candy	29	-1	19.5	18	20.3	17	23.4
Exp. C Hard apricot	37	4	23.1	11	22.0	18	26.5
Subject mean		5	21.7	19	23.4	15	22.4
Galago 7							
Exp. A Hard prune	29	31	24.7	27	22.0	38	23.2
Exp. B Gelatin candy	71	14	23.5	24	26.8	29	29.3
Exp. C Hard prune	29	1	28.7	24	32.9	35	32.6
Subject mean		15	25.6	25	27.2	34	28.4
Galago 8							
Exp. A Hard apricot	19	10	25.4			28	24.1
Exp. B Hard prune	19	18	17.1	16	11.8	5	17.9
Subject mean		14	21.3	16	11.8	17	21.0
Grand mean		11 ²	23.1	21 ²	23.4	23 ³	24.3

¹ Positive values indicate that peak EMG activity of the muscle precedes peak EMG activity of the working-side superficial masseter. Negative values indicate the reverse condition. N is number of power strokes; SD is standard deviation.

² Grand mean values indicate that the peak EMG activity of the working-side deep masseter and balancing-side superficial masseter precede peak EMG activity of the reference muscle ($P \leq .01$).

³ Working hypothesis is not supported as peak EMG activity of the balancing-side deep masseter precedes peak EMG activity of working-side superficial masseter ($P < .01$).

TABLE 11. Summary data of mean differences (in milliseconds) in timing of peak EMG of the working and balancing-side deep and the balancing-side superficial masseters relative to the reference muscle

Subject	Working deep	Balancing superficial	Balancing deep
Baboon	47***	17***	-6*
Macaque	65**	17**	-20*
Owl Monkey	13*	-1	-11*
Galago	11**	21**	23 ¹

¹ Working hypothesis is rejected as peak EMG activity of the balancing-side deep masseter precedes peak EMG activity of working-side superficial masseter ($P < .001$).

* $P \leq .05$. ** $P \leq .01$. *** $P \leq .001$.

TABLE 12. Summary data of mean differences (in milliseconds) in timing of peak EMG activity of masseter muscles

Subject	Working deep precedes balancing deep	Working deep precedes balancing superficial	Balancing superficial precedes balancing deep
Baboon	52***	30***	23***
Macaque	85**	48**	37**
Owl Monkey	24*	14****	10*
Galago	-12 ¹	-10 ²	-2 ³

¹ Working hypothesis is rejected as peak EMG activity of balancing-side deep masseter precedes peak EMG activity of working-side deep masseter ($P \leq .05$).

² Working hypothesis is rejected as peak EMG activity of balancing-side superficial masseter precedes peak EMG activity of working-side deep masseter ($P \leq .06$).

³ Working hypothesis is rejected as peak EMG activity of balancing-side deep masseter precedes peak EMG activity of balancing-side superficial masseter ($P \leq .87$).

* $P \leq .05$. ** $P \leq .01$. *** $P \leq .002$. **** $P \leq .1$.

the working-side deep and balancing-side superficial masseters precede the reference muscle by 47 and 17 ms for baboons ($P \leq 0.001$), and by 65 and 17 ms for macaques ($P \leq 0.01$). Furthermore, peak EMG ac-

tivity of the working-side deep masseter precedes activity of the balancing-side superficial masseter on average by 30 ms in baboons ($P \leq 0.001$) and 48 ms in macaques ($P \leq 0.01$) (Table 12). In contrast,

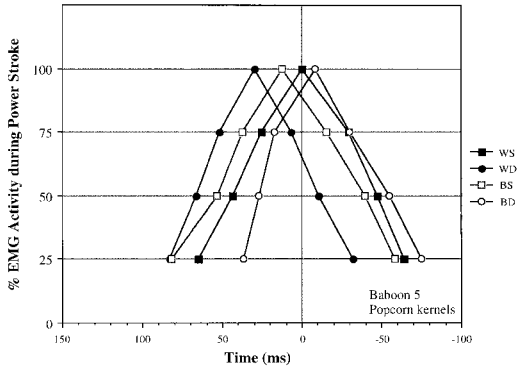


Fig. 6. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of popcorn kernels in baboon 5. The data for this figure are compiled from Experiments A, B, and C. The first muscle to reach peak activity is the working-side deep masseter, followed by the balancing-side superficial, working-side superficial, and balancing-side deep masseters. The vertical line indicates peak activity in the reference muscle, whereas positive values indicate that a muscle reaches peak activity after the reference muscle. Symbols and abbreviations as in legend for Figure 4.

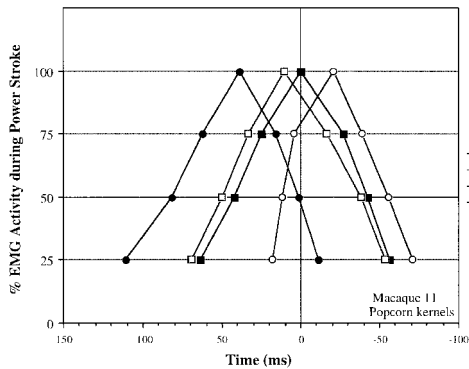


Fig. 7. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of popcorn kernels in macaque 11. The data for this figure are compiled from Experiments A and B. The first muscle to reach peak activity is the working-side deep masseter, followed by the balancing-side superficial, working-side superficial, and balancing-side deep masseters. The vertical line indicates peak activity in the reference muscle. Symbols and abbreviations as in legend for Figure 4.

peak EMG of the balancing-side deep masseter occurs after the reference muscle by 6 ms in baboons (mean = -6 ms; $P \leq 0.05$) and 20 ms in macaques (mean = -20 ms; $P \leq 0.05$). Figures 6 and 7 indicate the

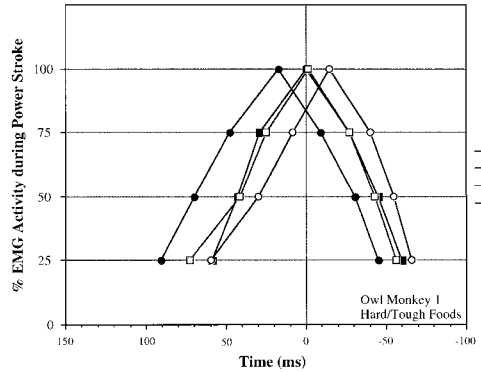


Fig. 8. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of hard/tough foods in owl monkey 1. The data for this figure are compiled from Experiments A and B. The first muscle to reach peak activity is the working-side deep masseter, followed by the near simultaneous activity of the working- and balancing-side superficial masseters, followed by the balancing-side deep masseter. The vertical line indicates peak activity in the reference muscle. Symbols and abbreviations as in legend for Figure 4.

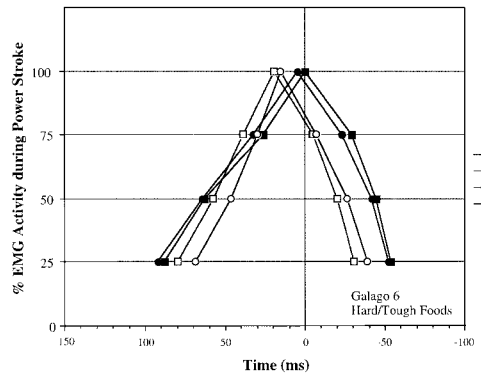


Fig. 9. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of hard/tough foods in galago 6. The data for this figure are compiled from Experiments A, B, and C. Unlike baboons, macaques, and owl monkeys, in thick-tailed galagos the balancing-side deep and superficial masseters reach peak activity first. The vertical line indicates peak activity in the reference muscle, which unlike the situation in the above anthropoids, is the last muscle to reach peak activity in thick-tailed galagos. Symbols and abbreviations as in legend for Figure 4.

timing of the masseters for baboon 2 and macaque 11. Note the considerable similarity between these two figures.

Owl monkeys. The mean timing differences for 12 separate experiments on two

different subjects are presented in Table 9. Similar to baboons and macaques, the data indicate that on average peak EMG of the working-side deep masseter precedes the reference muscle (mean = 13 ms; $P \leq 0.05$). Unlike macaques and baboons (and galagos), however, peak EMG of the balancing-side superficial masseter peaks 1 ms *after*, not well before, the reference muscle. Not surprisingly, this -1 ms mean value is not statistically significant. However, the data indicate an important difference in the recruitment patterns of the superficial masseters between owl monkeys 1 and 2. Similar to baboons and macaques (and galagos), activity of the balancing-side superficial masseter for owl monkey 2 ordinarily peaks before the reference muscle (mean = 6 ms; $P \leq 0.05$). In contrast, owl monkey 1 is unusual in that the balancing-side superficial masseter EMG peaks after the reference muscle (mean = -7 ms; $P > 0.05$) (Table 11).

Similar to baboons and macaques, for owl monkeys peak EMG activity of the working-side deep masseter precedes activity of the balancing-side superficial masseter (mean = 14 ms; $P \leq 0.05$) (Table 12), and peak EMG activity of the balancing-side deep masseter occurs after the reference muscle (mean = -11 ms; $P \leq 0.05$). Finally, Figure 8 indicates the relative timing of the various muscles for owl monkey 1. This subject exhibits, as described above, an unusual pattern for the two superficial masseters relative to one another. Note, however, the general similarity in the firing pattern of the deep masseters in all anthropoid subjects (Figs. 6-8). The working- and balancing-side deep masseters are the first and last muscles, respectively, to reach peak EMG activity.

Thick-tailed galagos. The mean timing differences for eight separate galago experiments on three different subjects are presented in Table 10. The data indicate that on average peak EMG of the working-side deep, balancing-side superficial, and balancing-side deep masseters precede the reference muscle by 11, 21, and 23 ms, respectively. Similar to anthropoids the first two mean values are positive and statistically significant ($P \leq 0.01$), but unlike anthropoids, the latter mean value is also positive, demonstrating that in

galagos the balancing-side deep masseter is not the last muscle to reach peak activity. Instead, it is one of the first muscles to reach peak activity. Furthermore, and again unlike the anthropoids, for galagos the balancing-side superficial masseter reaches peak EMG activity prior to the working-side deep masseter (mean = 9 ms, $P \leq 0.04$). Thus, in contrast to the firing pattern determined for anthropoids, for galagos the working-side deep masseter is not the first nor is the balancing-side deep masseter the last to reach peak EMG activity. Finally, and once again unlike anthropoids, for galagos the balancing-side deep masseter peaks 2 ms prior to the balancing-side superficial masseter. This mean value is small and not statistically significant (Table 12), suggesting that these two muscles reach peak activity more or less at the same time.

Summary of firing patterns. Tables 11 and 12 indicate quite clearly that for these anthropoids the first muscle to reach peak EMG activity is the working-side deep masseter, and the last muscle to reach peak activity is the balancing-side deep masseter. In contrast, for galagos, the first muscle to reach peak activity is the balancing-side deep (Table 11) although its timing is not significantly different from that of the balancing-side superficial masseter. Furthermore, in galagos the last muscle to reach peak activity is the reference muscle, the working-side superficial masseter.

Note in Table 12 that for the anthropoids the mean values for the three variables listed are all positive and they decrease in value from left to right. Furthermore, with a single exception, the anthropoid values are all statistically significant ($P \leq 0.05$). In contrast, for galagos the mean values for the three variables in Table 12 are all negative, and they become less negative, i.e., they increase algebraically from left to right. Two of these three mean values, however, are not statistically significant.

DISCUSSION

W/B EMG ratios and testing the allometric constraint-muscle recruitment hypothesis

The data presented in Tables 2-6 refute the allometric constraint hypothesis (hy-

pothesis 4) as this hypothesis predicts that the W/B EMG ratios are negatively correlated with overall body size. The data clearly demonstrate that the largest W/B ratios are not found in owl monkeys. Instead, owl monkeys (and macaques) have the smallest W/B EMG ratios for the superficial masseter. Similarly, a consideration of only the anthropoid data also provides no support for the allometric constraint hypothesis (hypotheses 5, 6, or 7). The results of this analysis are consistent with the results of our recently published mandibular corpus bone strain analysis (Hylander et al., 1998).

W/B EMG ratios and testing the symphyseal fusion-muscle recruitment hypothesis

The symphyseal fusion hypothesis predicts that although anthropoids and galagos may recruit about the same percentage of working-side masseter force, and therefore exhibit a similar percentage of working-side masseter EMG activity, anthropoids recruit more balancing-side muscle force, and therefore anthropoids have W/B EMG ratios that are relatively small and similar to one another, whereas the galago W/B ratios are relatively large. The data, as summarized in Table 6 and Figure 5, support this prediction. For example, anthropoids and galagos exhibit 65% to 75% of peak average EMG activity of their working-side masseters during forceful mastication. Moreover, galagos have the largest W/B ratios for both the superficial and deep masseters. However, as indicated in Tables 2–5, for the superficial masseter there is extensive overlap of the individual experiment W/B ratios between galagos and anthropoids. In contrast, for the deep masseter there is no overlap of the W/B ratio values between galagos and anthropoids. Therefore, the only clear difference in W/B ratios between galagos and anthropoids is associated with the deep masseter. This in turn supports the hypothesis that for anthropoids, symphyseal fusion and transversely-directed muscle force are functionally linked (hypothesis 2).

An alternative explanation of our data is that when the W/B EMG ratios are small, as in anthropoids, this may not be due to large

contributions of force from the balancing-side masseter, but instead is due to small contributions of force from the working-side masseter. We find this alternative explanation to be highly unlikely for the following reasons.

First, an analysis of facial bone strain in macaques indicates the occurrence of relatively large principal and shear strains along the anterior portion of the zygomatic arch during incision, isometric biting, and mastication (Hylander et al., 1992; Hylander and Johnson, 1997). As strains in the macaque zygomatic arch are most plausibly linked to ipsilateral masseter force, this indicates that if the working-side masseter is only weakly recruited during forceful chewing and biting (e.g., less than 20% of peak force), in those hypothetical instances when the masseter is actually strongly recruited (e.g. greater than 80% of peak force), strains in the zygomatic arch would be increased greatly (quadrupled?), resulting in structural failure of the zygomatic arch. This scenario strikes us as very unlikely.

Second, if we accept the alternative hypothesis that the masseter is only weakly recruited during mastication, incision and isometric molar biting, then it follows that the recruitment of maximum force from the masseter occurs during some behavior other than chewing and biting. We know of no such data to support this hypothesis and, therefore, are compelled to accept the more plausible hypothesis that the primary function of the masseter muscle is to generate bite force during chewing and biting.

Parenthetically, the macaque zygomatic-arch strain data demonstrate that the balancing-side strains are almost as large as the working-side strains, supporting the hypothesis that the balancing-side masseter of anthropoids is strongly recruited during forceful mastication. Furthermore, the W/B zygomatic-arch strain ratios average about 1.1, and predictably this value falls within the average W/B EMG ratios of macaques for the superficial and deep masseters (1.4 and 1.0, respectively). Thus, both the bone strain and EMG data are fully consistent with each other. Finally, we have established that the magnitude of peak masseter EMG is intensely correlated with peak mas-

seter force during the power stroke of mastication (Hylander and Johnson, 1989, 1993). This finding increases the likelihood that our W/B ratio data provide accurate information about the recruitment of relative masseter force.

Based on the above constellation of evidence, we argue that when primates engage in forceful chewing behaviors, small W/B EMG ratios are best interpreted as indicating large contributions of force from the balancing-side masseter, just as large W/B EMG ratios are best interpreted as indicating small contributions of force from the balancing-side masseter.

In summary, of the three symphyseal fusion hypotheses (hypotheses 1, 2, and 3), the data provide strong support for hypothesis 2, refute hypothesis 3, and seriously weaken hypothesis 1. An EMG analysis of the entire jaw adductor mass is arguably needed before completely rejecting hypothesis 1. Furthermore, as the superficial masseter is a relatively large muscle and as we have only sampled EMG activity from its central portion, sampling from multiple locations throughout this muscle is also arguably necessary before completely refuting hypothesis 1. We were unable to execute such an analysis due to the extremely complex nature of such an undertaking.

Differential firing patterns and the symphyseal fusion-muscle recruitment hypothesis

Previous work on macaques and baboons suggests that they share a common jaw-muscle firing pattern that causes their mandibles to experience wishboning during mastication (Hylander and Johnson, 1994). The working hypothesis predicts that owl monkeys also have this pattern and galagos do not.

The data in Tables 7–12 indicate quite clearly that the deep masseter firing pattern for galagos is quite different from that for macaques and baboons, whereas the firing pattern for owl monkeys is very similar to the one for baboons and macaques, i.e., for all three anthropoids, the first muscle to reach peak activity is the working-side deep, and the last to reach peak activity is the balancing-side deep. For galagos, the

balancing-side superficial and deep masseter reach peak activity first, and the working-side superficial masseter reaches peak activity last. Thus, as illustrated in Figures 6–9, a major difference in firing patterns between thick-tailed galagos and the anthropoids is related to the behavior of the deep masseters. Similar to the data on W/B EMG ratios, the firing pattern data support the hypothesis that symphyseal fusion and transversely-directed muscle force are functionally linked (hypothesis 2). That is, unlike anthropoids, both the W/B ratio and firing pattern data for the balancing-side deep masseter suggests that the galago symphysis experiences little if any wishboning. This is because the overall bending moment that causes wishboning is very small simply because the force associated with this moment, i.e., the force from the balancing-side deep masseter, is so small.

Differential firing patterns of the superficial masseter

With the exception of one of the owl monkeys (owl monkey 1), the data indicate that for all primate subjects the balancing-side superficial masseter reaches peak activity *before* peak activity of the working-side superficial masseter. This appears to be a typical mammalian pattern, and is importantly related to how mammals accomplish a combination of vertical and transverse jaw movements during the power stroke of mastication (Weijjs, 1994). In owl monkey 1, however, peak activity of the balancing-side superficial masseter occurs at or slightly *after* peak activity of the working-side superficial masseter. Moreover, an analysis of the firing patterns of the deep masseter (this study) and temporalis muscles (W.L. Hylander, C.F. Ross, and K.R. Johnson, unpublished data) reveals no other unusual firing patterns for this subject with the exception that the amount of asynchrony in EMG activity between the working- and balancing-side temporalis muscles is much greater in owl monkey 1 than it is in owl monkey 2. Presumably this more pronounced asynchrony enables owl monkey 1 to engage in relatively normal chewing movements despite the reversed timing pattern of its superficial masseters. As owl monkey 1 did not exhibit any

obvious pathology of the teeth or jaws, we have no explanation as to why the firing pattern of the superficial masseter in this subject deviates from that found in all other anthropoid subjects.

Allometry and the W/B ratio of the superficial masseter

The data in Tables 2–4 indicate that for baboons the W/B ratios of the superficial masseter (grand mean = 1.9) tend to be somewhat larger than those ratios for the much smaller-sized anthropoids (grand means = 1.4 for both macaques and owl monkeys). Earlier work on macaques indicates that W/B ratios of masseter force become smaller as subjects chew more and more forcefully (Hylander et al., 1992). Moreover, as the popcorn kernels were likely much easier for the baboons to chew as compared to macaques because of the much larger jaw muscles of baboons, perhaps the baboons did not come close to recruiting maximum levels of balancing-side muscle force during the chewing of hard kernels. If so, it is likely that the baboon W/B ratios in Table 2 are larger than what they would have been had the baboons chewed more mechanically resistant foods. This in turn suggests that if the baboons had chewed more forcefully, perhaps their W/B ratios would not have overlapped the galago values. Nevertheless, as the W/B ratios for the superficial masseter of galagos also overlapped ratio values for macaques and owl monkeys, it is highly unlikely that this problem has had any major influence on our general conclusion that galagos and anthropoids do not consistently differ in their W/B ratios for the superficial masseter during forceful chewing.

Wishboning and the balancing-side deep masseter

In 1994 we discussed the various external forces and moments associated with wishboning of the macaque mandible during mastication (Hylander and Johnson, 1994). These forces (Fig. 10) are the laterally-directed component to the bite force (F_b) (along the working side) and the opposite laterally-directed component to the balancing-side jaw muscle force (F_{mb}). Residual

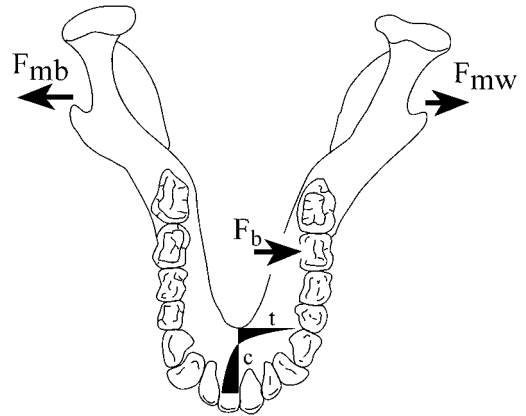


Fig. 10. Lateral bending or wishboning of the macaque mandibular symphysis. F_b , transverse component to the bite force; F_{mb} , transverse component to the balancing-side jaw-closing muscle force; F_{mw} , transverse component to the working-side jaw-closing muscle force. These three forces wishbone the mandible. The length of the arrows does not indicate the relative magnitude of bite and muscle forces; t, tensile bending stress; c, compressive bending stress. The darkly shaded areas along the symphysis indicate the distribution of bending stress for a symmetrical curved beam. In contrast to the situation for straight beams, note that the distribution of bending stress is markedly nonlinear. The tensile stress along the surface of the lingual aspect of the symphysis greatly exceeds the compressive stress along the surface of the labial aspect of the symphysis. (From Hylander and Johnson, 1994.)

force associated with the relaxing working-side jaw adductors (F_{mw}) also probably contributes to wishboning. An important aspect of wishboning is that it occurs late in the power stroke of mastication, and it is due mainly to increased recruitment of the balancing-side deep masseter at a time when force from the balancing-side superficial masseter and medial pterygoids (and also balancing-side lateral pterygoids?) have rapidly declined.¹

The EMG data provide strong evidence for the hypothesis that thick-tailed galagos

¹The lateral pterygoid muscles in primates appear to have a biphasic activity during mastication, i.e., they are active during both jaw opening and the power stroke. It has been hypothesized that the medially-directed components of force from the balancing-side medial and lateral pterygoids prevents the laterally-directed component of force of the balancing-side superficial masseter from causing wishboning of the symphysis. This may be why wishboning ordinarily does not occur earlier in the power stroke, a time when all of these muscles are highly active. Instead, wishboning occurs late, at a time when force from the balancing-side medial and lateral pterygoids and superficial masseter is rapidly decreasing and the balancing-side deep masseter force is rapidly increasing or has peaked (Hylander and Johnson, 1994).

do not significantly wishbone their mandibles during mastication. This is because their balancing-side superficial and deep masseters (Table 12), as well as their medial pterygoids (cf. Hylander and Johnson, 1994; Weijs, 1994), likely contract in a near synchronous fashion, which in effect counteracts moments that tend to wishbone their symphysis. Moreover, galagos recruit relatively low levels of force from their balancing-side deep masseter. Whereas the deep masseter W/B ratio is about 1.0 for anthropoids, it is greater than 4.0 for galagos. Furthermore, although anthropoids on average generate about 60% of peak force from their balancing-side deep masseter, galagos generate only about 25% of peak force.

Finally, in an effort to test further the symphyseal fusion-muscle recruitment hypothesis, we are currently analyzing EMGs recorded from the superficial and deep masseters of North American opossums (*Didelphis virginia*) (W.L. Hylander, A.W. Crompton, and K.R. Johnson, unpublished data). Although the mandibular symphysis of opossums is apparently stronger and less mobile than the galago symphysis (Beecher, 1977), it is similar to galagos in that it is unfused. Our preliminary data indicate that during forceful chewing the W/B EMG ratio for the superficial masseter of opossums is small (grand mean = 1.2), and thus very similar to that of anthropoids (also, cf. Crompton, 1985, 1995; Crompton and Hylander, 1986). Although compared to galagos the W/B ratio for the deep masseter of opossums is also small (grand mean = 1.8), this value is significantly larger than the anthropoid values. Most importantly, however, opossums do not exhibit the masseter firing pattern associated with wishboning. Instead, they have a masseter firing pattern very similar to that of galagos.

Thus, the very small W/B ratios of the superficial masseter of opossums suggest that an unfused symphysis and relatively small amounts of vertically-directed balancing-side muscle force are not functionally linked (cf. hypotheses 1 and 3). Moreover, the somewhat small W/B ratio for the deep masseter of opossums appears to weaken one aspect of hypothesis 2. On the other hand, the opossum timing data indicate the

absence of the jaw-muscle firing pattern that causes wishboning of the symphysis, which in turn supports hypothesis 2.

Dorsoventral shear, wishboning, symphyseal fusion, and ontogenetic timing

Ravosa has argued that both wishboning and dorsoventral shear are functionally linked to symphyseal fusion in primates, and that the relative importance of each is linked to the ontogenetic timing of symphyseal fusion (Ravosa and Simons, 1994; Ravosa, 1996). When symphyseal fusion occurs relatively early in ontogeny, prior to the initiation of weaning, fusion is hypothesized to be a structural adaptation to counter wishboning stress associated with post-weaning chewing behaviors. When fusion occurs relatively late in ontogeny, well after weaning, fusion is hypothesized to be an adaptive response to counter increased dorsoventral shear stress in a species that does not ordinarily wishbone its mandible during mastication.

The EMG data from this study support the hypothesis that early fusion and wishboning are linked in that our anthropoid subjects exhibit the deep masseter firing pattern associated with wishboning, whereas the thick-tailed galagos do not. The lack of a wishboning firing pattern in galagos also supports the suggestion that the prosimian mandibular symphysis is especially designed to resist dorsoventral shear stress (Beecher, 1977, 1979). Until jaw-muscle recruitment patterns of additional prosimians have been determined, however, it is premature to assume that the firing pattern of thick-tailed galagos is typical for all prosimian primates.² An EMG analysis of masseter firing patterns in those prosimians with well-buttressed and partially-fused symphyses would be a good test of the Beecher and Ravosa hypotheses. That is, these hypotheses predict that the wishboning firing pattern is not present in, for example, indriid or *Hapalemur* species. The Ravosa hy-

²We are planning to initiate an EMG analysis of the relative force recruitment and firing pattern of the superficial and deep masseter muscles in *Lemur catta* (W.L. Hylander, C.J. Vinyard, and K.R. Johnson, unpublished data).

pothesis makes this prediction since partial fusion in these taxa occurs well after weaning. Finally, masseter firing patterns for anthropoids, as well as bone strain analyses of the macaque mandibular symphysis (Hylander, 1984), do not support Beecher's hypothesis linking symphyseal fusion in anthropoids to dorsoventral shear stress.

Wishboning and humans

As noted elsewhere, there may be a problem with the hypothesis that anthropoid symphyseal fusion and wishboning are linked in that although the human symphysis is fused, the deep masseter wishboning firing pattern may not be present in humans (Hylander and Johnson, 1994). EMG studies suggest that humans do not exhibit the late activity of the balancing-side deep masseter (cf., van Eijden et al., 1993). Instead, the balancing-side deep masseter firing pattern is more similar to that found in thick-tailed galagos in that this muscle reaches peak activity early in the power stroke. On the other hand, similar to anthropoids and unlike galagos, peak EMG activity of the balancing-side deep masseter in humans occurs after peak activity of the balancing-side superficial masseter (van Eijden et al., 1993). Moreover, and perhaps most importantly, unlike galagos and similar to other anthropoids, humans recruit a relatively large amount of force from the balancing-side deep masseter (cf. Belser and Hannam, 1986). Thus, there is some reason to believe that the human mandible may also experience a type of wishboning during the power stroke of mastication (Hylander and Johnson, 1994). Nevertheless, the human data suggest that not all anthropoids have the same deep masseter firing pattern as found in baboons, macaques and owl monkeys.

We are currently in the planning process of doing an EMG analysis of the superficial and deep masseter in humans so as to confirm the results of van Eijden et al. (1993) (W.L. Hylander, C.E. Wall, C.F. Vinyard, and K.R. Johnson, unpublished data). An interesting and related question, of course, is whether humans are unique among living anthropoids in not having this firing pattern, and if so, this would suggest that the human lineage has secondarily lost this fir-

ing pattern. Obviously, an EMG analysis of the masseter of chimpanzees, gorillas or orangutans would provide an important test of this hypothesis.

CONCLUSIONS

An analysis of the W/B EMG ratios of the superficial and deep masseter for baboons, macaques, owl monkeys and thick-tailed galagos refute the allometric constraint-muscle recruitment hypothesis. The largest W/B ratios for the superficial and deep masseter are not found in owl monkeys. Instead, owl monkeys (and macaques) actually have the smallest W/B EMG ratios for the superficial masseter. Most importantly, the largest W/B EMG ratios for both the superficial and deep masseter are found among thick-tailed galagos, and the owl monkey W/B ratios for these muscles are very similar to those of baboons and macaques.

The symphyseal fusion-muscle recruitment hypothesis predicts that although both anthropoids and galagos recruit about the same percentage of working-side masseter force, and therefore exhibit the about the same percentage of peak EMG activity of their working-side masseters, anthropoids have W/B EMG ratios that are relatively small and similar to one another, and galagos have W/B ratios that are relatively large. Although the data indicate that galagos have the largest W/B ratios for both the superficial and deep masseters and that anthropoids have relatively small W/B ratios, the only sharp distinction in W/B EMG ratios between thick-tailed galagos and anthropoids is associated with the deep masseter. Furthermore, the analysis of masseter firing patterns indicates that whereas baboons, macaques and owl monkeys possess the deep masseter wishboning firing pattern, galagos do not. Thus, the data for W/B ratios and masseter firing patterns support the hypothesis that symphyseal fusion and transversely-directed muscle force are functionally linked in anthropoids.

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