

11 *Jaw adductor force and symphyseal fusion*

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Introduction

Research over the last 25–30 years has revealed a considerable amount about the basic mechanisms of mammalian mastication (e.g., van Eijden and Turkawski, 2001; Türker, 2002). This progress has been largely due to the development of new experimental procedures and techniques. On the other hand, there has been relatively little emphasis on employing these procedures and techniques so as to facilitate adaptive explanations for the evolution of the mammalian masticatory apparatus (Herring, 1993). It has been our intent over the last several years to do just that (Ross and Hylander, 1996; Hylander *et al.*, 1998, 2000, 2002, 2003; Ravosa *et al.*, 2000; Vinyard *et al.*, 2001, in press a; Wall *et al.*, 2002; Williams *et al.*, 2003). In recent years the functional morphology of the craniofacial region of primates and other mammals has attracted a significant amount of research interest (Weijs, 1994; Ross and Hylander, 1996, 2000; Spencer, 1998; Anapol and Herring, 2000; Daegling and Hylander, 2000; Dechow and Hylander, 2000; Herring and Teng, 2000; Hylander *et al.*, 2000; Lieberman and Crompton, 2000; Ravosa *et al.*, 2000). This is simply because there continue to be many unanswered research questions or problems. One persistent problem that has received a considerable amount of attention is related to the adaptive significance of symphyseal fusion in mammals. As noted by many, the ossification or fusion of the left and right sides of the lower jaw or dentaries has

occurred independently in many different mammalian lineages (e.g., Beecher, 1977). In spite of extensive morphological and comparative studies, there is little agreement as to the ultimate reasons for symphyseal fusion (Beecher, 1979; Scapino, 1981) – that is, whether or not certain diets are normally associated with the evolution of symphyseal fusion, and also whether symphyseal fusion is an outcome of allometric factors (Beecher, 1977; Scapino, 1981; Ravosa and Hylander, 1994). This lack of consensus has caused us to refocus our attention on the more immediate or proximate factors that are related to symphyseal fusion. More specifically, we have been attempting to determine if certain types of biomechanical situations or loading patterns are plausibly associated with symphyseal fusion.

When most mammals chew food, they typically do so unilaterally but have bilateral recruitment of their jaw-adductor muscles, i.e., both the working-side (chewing side) and the balancing-side (or non-chewing side) jaw muscles produce varying amounts of jaw muscle force. This fact has important consequences as to how various portions of the mandible are loaded, and is particularly important for loading of the mandibular symphysis. This is simply because during unilateral chewing or biting, muscle force from the balancing-side jaw muscles must be transferred through the symphysis to the working side, and this in turn results in various sorts of symphyseal loading regimes (Hylander, 1984).

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. Similarly, 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 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 data indicate that for all species analyzed, peak working-side corpus strains are relatively large and similar in magnitude. Moreover, for these two anthropoid species the balancing-side strains are only slightly smaller than their working-side strains, whereas for galagos

the balancing-side strains are much smaller than both their working-side strains and the balancing-side strains of anthropoids. As balancing-side corpus strains are predominately the result of balancing-side muscle force (Hylander, 1977), these data indicate that compared to anthropoids, galagos apparently recruit much less balancing-side muscle force during mastication.

Macaques and owl monkeys have a fully fused mandibular symphysis, which is the derived condition for crown anthropoids, whereas adult thick-tailed galagos have an unfused symphysis, which is a retention of the primitive mammalian condition. Furthermore, unlike the rigid symphysis of anthropoids, 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–muscle recruitment hypothesis. Furthermore, the strain data refute the allometric constraint–muscle recruitment hypothesis (Hylander *et al.*, 1998).

Muscle force direction, 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 (Ravosa and Hylander, 1994; Ravosa and Simons, 1994; Ravosa, 1996; Hylander *et al.*, 1998, 2000, 2002; Hogue and Ravosa, 2001). If vertically directed, then a likely functional correlate of this force is an 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 a structural adaptation to prevent mechanical failure by more effectively resisting increased symphyseal stresses due to these particular shearing and bending regimes.

If the increased balancing-side 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 adaptation to prevent its structural failure by more effectively resisting increased symphyseal stresses due to this particular bending regime.

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

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. Towards this end, we summarize here the results of a detailed electromyographic (EMG) analysis of the superficial and deep masseters of baboons, macaques, owl monkeys, thick-tailed galagos, and ring-tailed lemurs. Unlike anthropoids and similar to thick-tailed galagos, ring-tailed lemurs have an unfused mandibular symphysis. Compared to galagos, however, ring-tailed lemurs have a stiffer and stronger symphysis (Beecher, 1977, 1979), and these differences in morphology may be reflected in corresponding differences in the motor patterns of their jaw muscles during mastication. This EMG analysis enables us to characterize activity patterns for one portion of the jaw-adductor muscle mass that has a relatively large vertical orientation, the superficial masseter, and one portion that has a relatively large transverse orientation, the deep masseter (Hylander and Johnson, 1994). Data such as these can provide insight as to whether there are major differences in muscle recruitment and firing patterns during mastication, and by inference in symphyseal loading patterns, between anthropoids on the one hand and strepsirhines with unfused symphyses on the other.

Hypothesis 1

In contrast to anthropoids, thick-tailed galagos and ring-tailed lemurs recruit relatively less overall balancing-side muscle force during the power stroke of mastication: i.e., bite force in galagos and lemurs 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 and lemurs are predicted to

have relatively large working-side/balancing-side (W/B) ratios of peak EMG values for *both* the superficial and deep masseter muscles. If true, this outcome would support the hypothesis that increased vertically and transversely directed balancing-side muscle forces are linked to the evolution of symphyseal fusion in anthropoids. Furthermore, it would also support the hypothesis that symphyseal fusion is linked to symphyseal stress due to some combination of (1) dorsoventral shear, (2) frontal bending of the symphysis associated with twisting of the mandibular corpora, and (3) lateral transverse bending or wishboning.

Hypothesis 2

On the other hand, and similar to anthropoids, the galagos and lemurs may recruit a substantial amount of force from their balancing-side superficial masseter (Hylander *et al.*, 1992; 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 anthropoids and strepsirhines have similar or overlapping W/B EMG ratio values for the superficial masseter. For the deep masseter, however, this hypothesis predicts that anthropoids have a small W/B ratio whereas thick-tailed galagos and ring-tailed lemurs have a large W/B ratio. This outcome would support 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. Furthermore, it would also support the hypothesis that symphyseal fusion is linked to symphyseal stress due to wishboning.

Hypothesis 3

Another possibility is that, similar to anthropoids, thick-tailed galagos and ring-tailed lemurs 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 anthropoids and strepsirhines have similar or overlapping W/B ratios for the deep masseter, but for the superficial masseter anthropoids will have a small W/B ratio, and thick-tailed galagos and ring-tailed lemurs will have a large W/B ratio. This outcome would support the hypothesis that the evolution of symphyseal fusion in anthropoid primates is linked to increased vertically directed balancing-side muscle forces. Furthermore, it would support the hypothesis that symphyseal fusion is linked to symphyseal stress due to a combination of dorsoventral shear and frontal bending.

Masseter firing patterns and wishboning

We also propose to determine whether thick-tailed galagos, ring-tailed lemurs, and owl monkeys exhibit the macaque and baboon pattern of 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 late in the power stroke, at a time when vertically directed muscle force is rapidly declining during the most terminal portion of the power stroke (Hylander and Johnson, 1994). If it turns out that owl monkeys have this firing pattern whereas galagos and lemurs do not, this outcome would support the hypothesis that the evolution of symphyseal fusion in anthropoids is linked to transversely directed muscle forces.

In summary, the symphyseal fusion–muscle recruitment hypothesis (hypotheses 1, 2, and 3) predicts that anthropoids recruit relatively more balancing-side masseter force than do galagos and lemurs, and therefore that compared to these strepsirrhines the W/B EMG ratios of the superficial and/or deep masseters are smaller for anthropoids. Hypotheses 1 and 2 are also compatible with the hypothesis that, unlike thick-tailed galagos and ring-tailed lemurs, anthropoids have a deep masseter firing pattern that causes the mandibular symphysis to experience wishboning during mastication.

Materials and methods

Subjects

Five baboons (*Papio anubis*), four macaques (three *Macaca fascicularis* and one *Macaca fuscata*), two owl monkeys (*Aotus trivirgatus*), three thick-tailed galagos (two *Otolemur crassicaudatus* and one *Otolemur garnettii*), and four ring-tailed lemurs (*Lemur catta*) served as subjects. All subjects, which were either young adults or subadults, are described in detail elsewhere (Hylander *et al.*, 2000, 2002). 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.

EMG electrodes and electrode placement procedure

As many as eight fine-wire indwelling bipolar electrodes were placed within the left and right middle portion of the superficial and deep masseter muscles according to procedures outlined elsewhere (Hylander *et al.*, 2000) (Fig. 11.1). All electrodes were inserted with the subjects under light sedation.

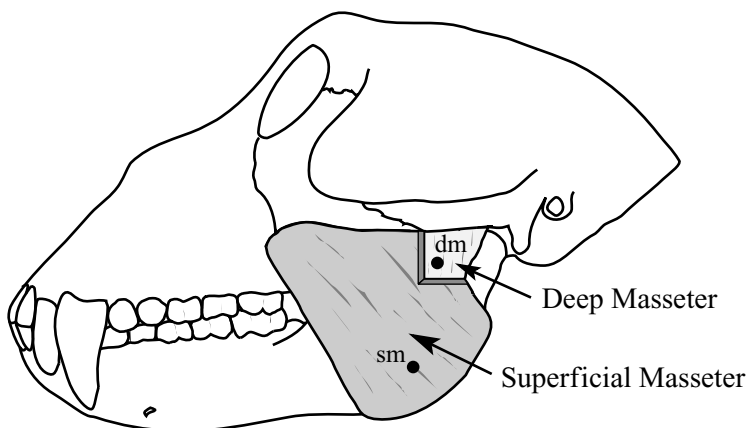


Figure 11.1. Lateral view of a macaque skull and the superficial and deep portions of the masseter muscle. The solid black dots indicate the location of the bipolar fine-wire electrodes in the deep (dm) and superficial (sm) portions of the masseter (from Hylander *et al.*, 2000).

Recording procedure

Prior to recovery from sedation, the subject was placed in a restraining chair (baboons, macaques, and lemurs) 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 100–3000 Hz) and then recorded on an FM tape recorder at 15 inches (0.38 m) per second. Details of the recording procedure are the same as described previously (Hylander and Johnson, 1989, 1994). The data presented here are based on 55 separate experiments (16 baboon, 10 macaque, 12 owl monkey, 8 galago, and 9 lemur experiments). All EMG data were recorded as subjects vigorously chewed various food items. 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.

EMG quantification

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),

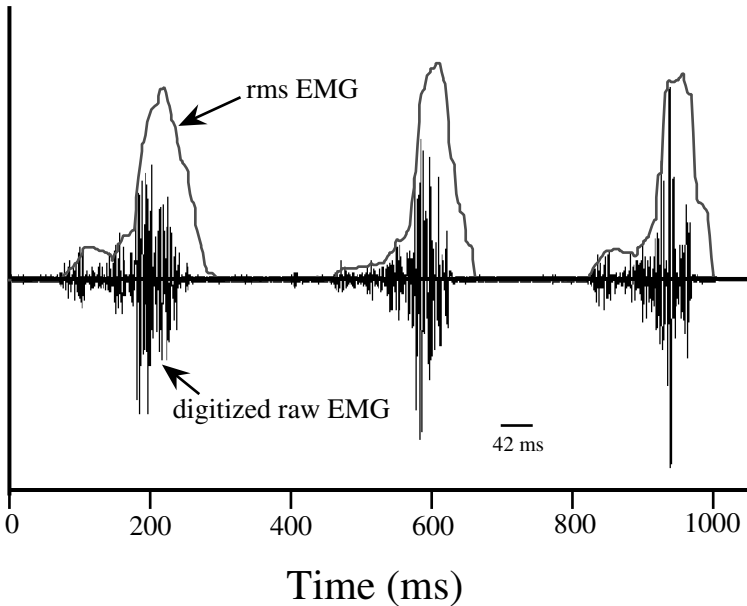


Figure 11.2. Digitized raw EMGs and the corresponding root-mean-square (rms) EMGs for the working-side superficial masseter of a male macaque during mastication of popcorn kernels. The rms values were calculated using a 42 ms time constant for reasons outlined in Hylander and Johnson (1993). The use 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).

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. The digitized values were then read back into the microcomputer for subsequent processing and analysis.

Raw digitized EMG values (Fig. 11.2) were first filtered with a digital Butterworth band-pass filter (100–3000 Hz). The EMG was then rectified and smoothed by calculating the root-mean-square (rms) values from the raw digitized values for a 42 millisecond (ms) time constant (Fig. 11.2) (Hylander and Johnson, 1993). The rms values were calculated in 2 ms intervals for the entire chewing sequence. For each electrode and power stroke we then identified the maximum peak rms value for each experiment. The peak values for each experiment were then scaled by assigning a value of 1.0 to the largest value, and the

remaining 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 values for the superficial and deep masseter muscles were then divided by the scaled peak balancing-side EMG value. We refer to this value as the W/B EMG ratio. Means and standard deviations of this variable were determined for each experiment and subject. For each primate group grand means of the W/B EMG ratio were calculated based on experiment mean values. For reasons outlined elsewhere (Hylander and Johnson, 1994), a log transformation of the data was performed, and the transformed mean values of the W/B ratios for the left and right sides were combined and then transformed back to their original scale.

Due to inherent problems associated with the statistical testing of ratios, we intend to focus the analysis on the grand means and experiment means of these ratios. One of our main goals is to determine if the W/B ratios of the superficial and/or deep masseter in galagos and lemurs *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-side and balancing-side deep masseters and the balancing-side superficial 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-side and balancing-side deep masseters, (2) the balancing-side superficial and deep masseters, and (3) the working-side deep and balancing-side superficial masseters.

Another main goal is to determine whether the masseter firing pattern for baboons, macaques, and owl monkeys differs from that for galagos and lemurs, and also whether only the anthropoids possess the masseter firing pattern thought to be associated with wishboning of the macaque symphysis (Hylander *et al.*, 1987). The wishboning firing pattern is characterized by peak activity of the working-side deep and balancing-side superficial masseters *preceding* peak activity of the working-side superficial masseter, and by peak activity of the balancing-side deep masseter *following* peak activity of the working-side superficial masseter (Hylander and Johnson, 1994) (Figs. 11.3 and 11.4). Thus, as

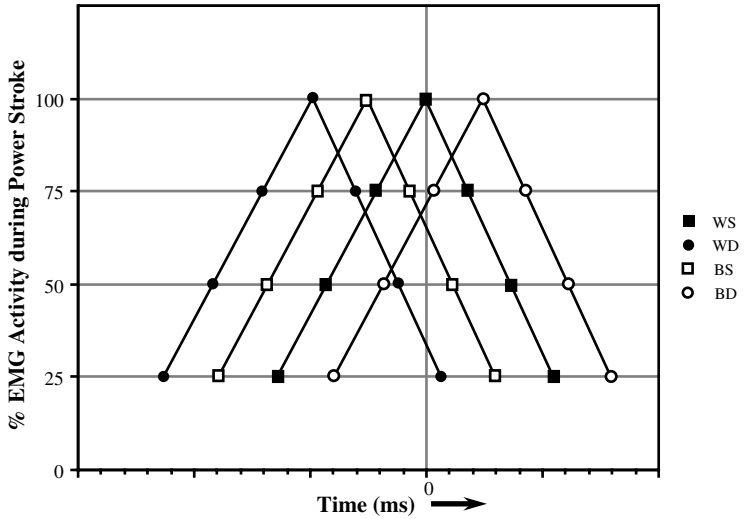


Figure 11.3. Predictions of masseter firing pattern associated with wishboning of the symphysis. The working hypothesis predicts the occurrence of this pattern only in those primates with a fully fused mandibular symphysis, i.e., in extant anthropoids, but not in those prosimians with a highly mobile 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. Abbreviations: WS, working-side superficial masseter; WD, working-side deep masseter; BS, balancing-side superficial masseter; BD, balancing-side deep masseter (from Hylander *et al.*, 2000).

noted earlier, this firing pattern results in the balancing-side deep masseter reaching peak force late in the power stroke, 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. All tests of significance were of the grand means. The mean timing differences in peak EMGs between muscles were tested for significance at the 95% level by using a nonparametric 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.

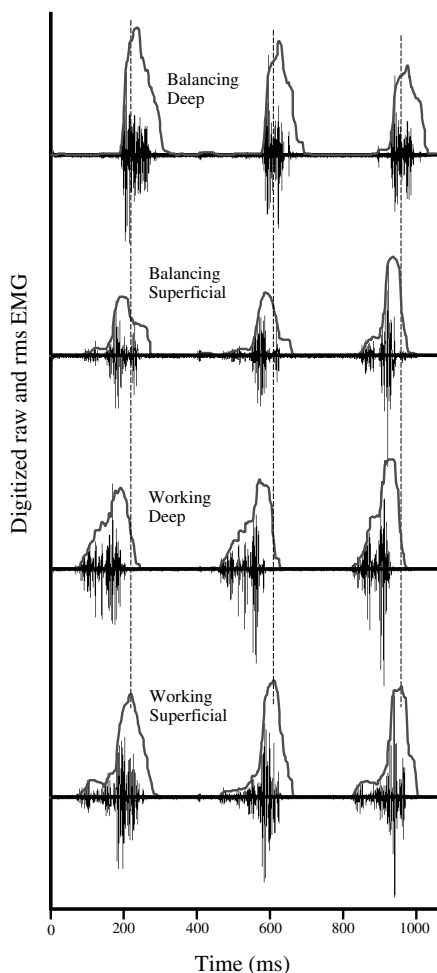


Figure 11.4. Digitized raw and rms EMGs of the working-side and balancing-side deep and superficial masseters in a male macaque during mastication of popcorn kernels. On average the working-side deep masseter is the first muscle to reach peak activity, and the balancing-side deep masseter is the last 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 (from Hylander *et al.*, 2000).

Table 11.1. *Summary data of mean W/B ratios*

Subject	Superficial masseter				Deep masseter			
	<i>n</i>	Mean	SD	Range	<i>n</i>	Mean	SD	Range
Baboon	15	1.9	0.40	1.3 to 2.7	12	1.0	0.22	0.7 to 1.4
Macaque	8	1.4	0.25	1.2 to 1.8	7	1.0	0.20	0.7 to 1.3
Owl monkey	12	1.4	0.22	1.1 to 1.8	4	1.4	0.13	1.2 to 1.5
Thick-tailed galago	7	2.2	0.49	1.5 to 2.8	8	4.4	2.39	2.1 to 9.5
Ring-tailed lemur	9	1.7	0.70	1.3 to 3.1	9	2.4	0.99	1.8 to 3.4

Overall mean values are grand means based on the mean of all experiments for each species.

The experiment means are based on all power strokes within a chewing sequence.

n is the number of individual experiments, not the number of power strokes.

Results

Typically, some subjects simply refused to eat certain foods. All, however, chewed at least one of the hard or tough foods. Therefore, EMG data were recorded from all subjects during episodes of relatively forceful and vigorous mastication. We only present data recorded during the chewing of hard or tough foods so as to confine the EMG analysis to the relatively forceful sequences of 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 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 grossly distorted by one or two unusually large individual ratio values.

W/B EMG ratios

Table 11.1 presents the descriptive statistics of the W/B ratios for sequences of chewing hard or tough foods for baboons, macaques, owl monkeys, galagos, and lemurs.

Superficial masseter

For the superficial masseter the anthropoid W/B ratios are smaller than the W/B ratios for galagos, but not so for lemurs. The grand mean W/B ratios of baboons, macaques, owl monkeys, galagos, and lemurs are 1.9, 1.4, 1.4, 2.2, and 1.7, respectively. Moreover, there is a considerable overlap of the experiment mean values between the anthropoid and strepsirhine species. For example, the individual experiment mean values for anthropoids range from 1.1 to 2.7, whereas for the strepsirhines these values range from 1.3 to 3.4.

Deep masseter

For the deep masseter the anthropoid W/B ratios are unlike the W/B ratios for galagos, and lemurs. The W/B deep masseter ratios for baboons, macaques, owl monkeys, galagos, and lemurs are 1.0, 1.0, 1.4, 4.4, and 2.4, respectively. For anthropoids the mean W/B ratios for each experiment range from 0.7 to 1.5, whereas for the strepsirhines these values range from 1.8 to 9.5. Thus, there is no overlap whatsoever in the experiment mean values. 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 the average differences of the W/B ratios between the galagos and anthropoids.

Percentage EMG activity of the masseter

Figure 11.5 shows percent scaled EMG values for the working-side and balancing-side masseters during the chewing of hard or tough foods. In addition to indicating some of what has already been described for the W/B ratios, this figure demonstrates that on average the working-side muscles range from 55% to 75% for both the superficial and deep masseters. In contrast, the balancing-side muscles are more variable. For the balancing-side superficial masseter the values range from 32% to 55%. 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 and lemurs only recruit 25% and 30% of peak activity of the balancing-side deep masseter.

Masseter firing patterns of peak EMG

Table 11.2 presents the descriptive statistics for the firing patterns of the working-side and balancing-side masseters for baboons, macaques, owl monkeys, galagos, and lemurs during the chewing of hard or tough foods. This table

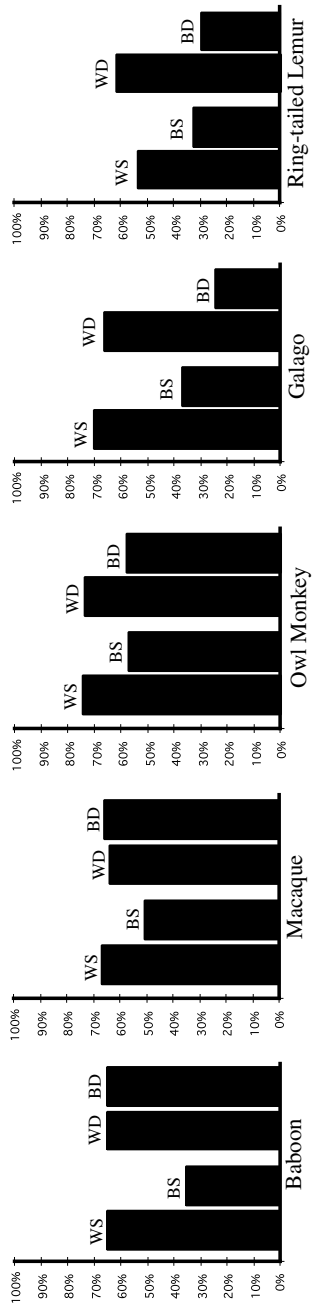


Figure 11.5. Bar graphs of average percent EMG activity for all primates during the chewing of hard and/or tough foods. Abbreviations: WS, working-side superficial; BS, balancing-side deep; BD, working-side deep; WD, working-side superficial; WD, balancing-side deep masseters (from Hylander *et al.*, 2000).

Table 11.2. Summary data of mean differences in timing (milliseconds) 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		
	<i>n</i>	Grand mean	SD	<i>n</i>	Grand mean	SD	<i>n</i>	Grand mean	SD
Baboon	13	47***	16.7	13	17***	14.1	13	-6*	9.1
Macaque	8	65**	17.1	8	17**	8.4	7	-20*	16.9
Owl monkey	4	13*	11.7	12	-1	11.4	4	-11*	9.0
Thick-tailed galago	8	11**	10.4	7	21**	6.3	8	23 ^a	11.7
Ring-tailed lemur	9	37**	18.5	9	14**	13.4	9	24 ^a	23.0

Overall mean values are grand means based on the mean of all experiments for each species.

The experiment means are based on all power strokes within a chewing sequence.

n is the number of individual experiments, not the number of power strokes.

* Significantly greater than zero ($P \leq 0.05$).

** Significantly greater than zero ($P \leq 0.01$).

*** Significantly greater than zero ($P \leq 0.001$).

^a Working hypothesis is rejected as peak EMG activity of the balancing-side deep masseter precedes peak EMG activity of working-side superficial masseter ($P < 0.01$).

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.

Positive values indicate that peak EMG of the muscle precedes peak activity of the reference muscle, and negative values indicate the reverse. Table 11.3 consists of the grand means of three additional timing variables for these five groups of primates. These variables are the time intervals between peak EMG of (1) the working-side 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 11.6–11.10 indicate the mean timing differences of the working-side and balancing-side masseter muscles throughout the power stroke for one subject from each of the five groups of primates. In addition to 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 data indicate that on average peak EMG of the working-side deep and balancing-side superficial masseters precede

Table 11.3. Summary data of mean differences in timing (milliseconds) of peak EMG activity of masseter muscles

Subject	Working deep precedes balancing deep			Working deep precedes balancing superficial			Balancing superficial precedes balancing deep		
	<i>n</i>	Grand mean	SD	<i>n</i>	Grand mean	SD	<i>n</i>	Grand mean	SD
Baboon	13	52***	16.0	12	30***	14.7	12	23***	9.9
Macaque	7	85**	20.8	7	48**	11.5	6	37**	17.6
Owl Monkey	4	24*	12.0	4	14†	11.9	4	10*	3.6
Thick-tailed Galago	8	-12 ^a	14.1	7	-10 ^b	10.3	7	-1	11.0
Ring-tailed Lemur	9	12**	6.4	9	22**	15.7	9	-9 ^c	13.9

Overall mean values are grand means based on the mean of all experiments for each species.

The experiment means are based on all power strokes within a chewing sequence.

n is the number of individual experiments, not the number of power strokes.

* Significantly greater than zero ($P \leq 0.05$).

** Significantly greater than zero ($P \leq 0.01$).

*** Significantly greater than zero ($P \leq 0.002$).

† Significantly greater than zero ($P \leq 0.1$).

^a Working hypothesis is rejected as peak EMG activity of balancing-side deep masseter precedes peak EMG activity of working-side deep masseter ($P \leq 0.05$).

^b Working hypothesis is rejected as peak EMG activity of balancing-side superficial masseter precedes peak EMG activity of working-side deep masseter ($P \leq 0.05$).

^c Working hypothesis is rejected as peak EMG activity of balancing-side deep masseter precedes peak EMG activity of balancing-side superficial masseter ($P \leq 0.05$).

the reference muscle by 47 ms and 17 ms for baboons ($P \leq 0.001$), and by 65 ms and 17 ms for macaques ($P \leq 0.01$). Furthermore, peak EMG activity 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 11.3). In contrast, 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 11.6 and 11.7 indicate the timing of the masseters for baboon 5 and macaque 11. Note the considerable similarity between these two figures.

Owl monkeys

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, 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. Similar to baboons and macaques, for owl monkeys peak EMG

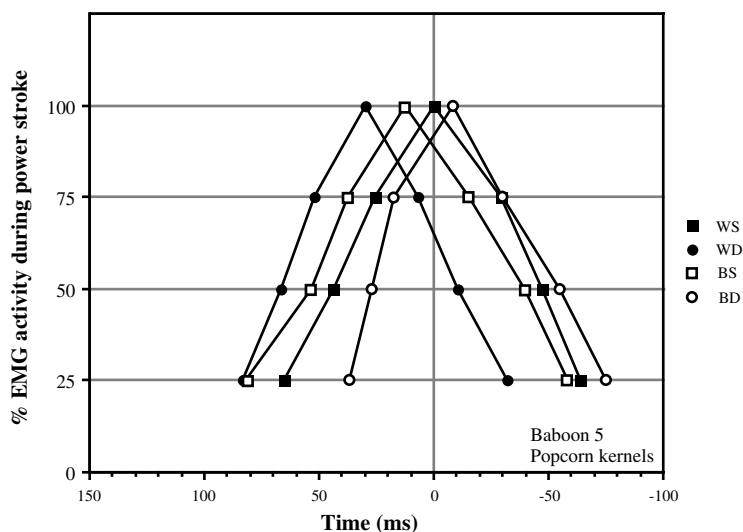


Figure 11.6. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of popcorn kernels in baboon 5. The first muscle to reach peak activity is the working-side deep masseter, followed by the balancing-side superficial, working-side superficial, and balancing-side deep masseters. The vertical line indicates peak activity in the reference muscle, the working-side superficial masseter. Positive timing values indicate that a muscle reaches peak activity prior to peak activity of the reference muscle, whereas negative values indicate peak activity after the reference muscle. Symbols and abbreviations as in Figure 11.3 (from Hylander *et al.*, 2000).

activity of the working-side deep masseter precedes activity of the balancing-side superficial masseter (mean = 14 ms; $P \leq 0.05$) (Table 11.3), and peak EMG activity of the balancing-side deep masseter occurs after the reference muscle (mean = -11 ms; $P \leq 0.05$). Finally, Figure 11.8 indicates the relative timing of the various muscles for one of our owl monkeys. This subject exhibits 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. 11.6, 11.7, and 11.8). The working-side and balancing-side deep masseters are the first and last muscles, respectively, to reach peak EMG activity.

Thick-tailed galagos

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 ms, 21 ms, and 23 ms, respectively. As in the anthropoids, the first two mean values are positive and statistically significant ($P \leq 0.01$), but

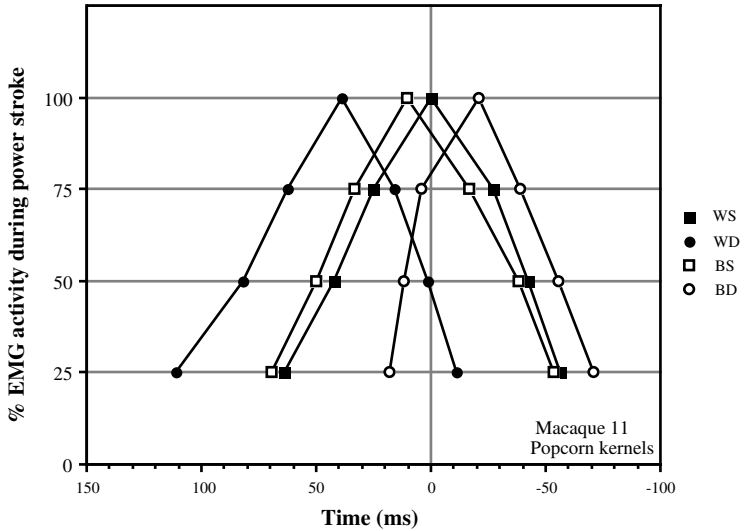


Figure 11.7. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of popcorn kernels in macaque 11. The first muscle to reach peak activity is the working-side deep masseter, followed by the balancing-side superficial, working-side superficial, and balancing-side deep masseters. The vertical line indicates peak activity in the reference muscle. Symbols and abbreviations as in Figure 11.3 (from Hylander *et al.*, 2000).

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, for galagos 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 = -10 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 1 ms prior to the balancing-side superficial masseter. This mean value is small and not statistically significant (Table 11.3), suggesting that these two muscles reach peak activity more or less at the same time.

Ring-tailed lemurs

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 37 ms, 14 ms, and 24 ms, respectively. As in anthropoids and galagos the first two mean values are positive and statistically significant

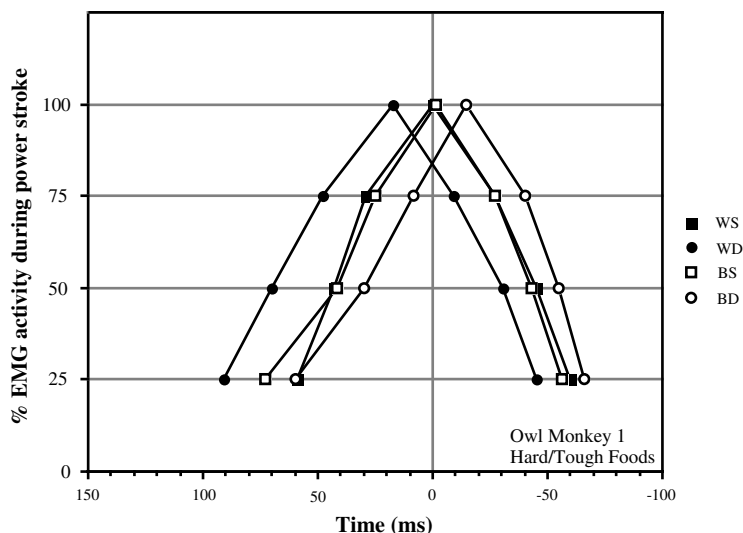


Figure 11.8. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of hard/tough foods in owl monkey 1. The first muscle to reach peak activity is the working-side deep masseter, followed by the near simultaneous activity of the working-side 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 Figure 11.3 (from Hylander *et al.*, 2000).

($P \leq 0.01$), but unlike anthropoids, the latter mean value is also positive, demonstrating that in lemurs (and galagos) the balancing-side deep masseter is not the last muscle to reach peak activity. Instead, for lemurs (and galagos) it reaches peak activity early in the power stroke. Furthermore, similar to anthropoids but unlike galagos, for lemurs the balancing-side superficial masseter reaches peak EMG activity after the working-side deep masseter (mean = 22 ms, $P \leq 0.01$). Thus, similar to the firing pattern determined for anthropoids, for lemurs the working-side deep masseter is the first to reach peak EMG activity. Finally and most importantly, and unlike anthropoids, for lemurs the balancing-side deep masseter peaks 9 ms prior to the balancing-side superficial masseter. This mean value is statistically significant (Table 11.3).

Summary of firing patterns

Tables 11.2 and 11.3 indicate quite clearly that for the anthropoids the first muscle to reach peak EMG activity is the working-side deep masseter and

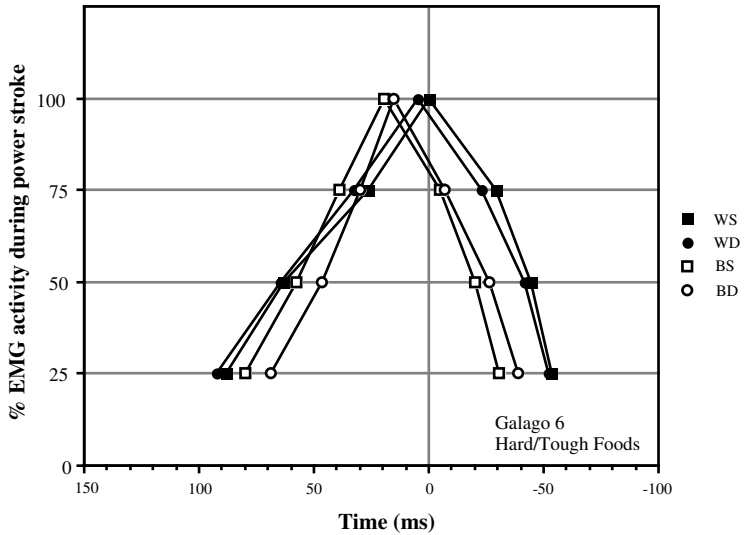


Figure 11.9. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of hard/tough foods in galago 6. Unlike baboons, macaques, and owl monkeys, in thick-tailed galagos the balancing-side deep and superficial masseters reach peak activity first. 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 Figure 11.3 (from Hylander *et al.*, 2000).

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 although its timing is not significantly different from that of the balancing-side superficial masseter. For lemurs the first muscle to reach peak activity is the working-side deep masseter. Most importantly, in galagos and lemurs the last muscle to reach peak activity is the reference muscle, the working-side superficial masseter.

Note in Table 11.3 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 11.3 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. Finally, for lemurs the first two variables are positive as in anthropoids, but the last is negative as in galagos. All three variables are statistically significant.

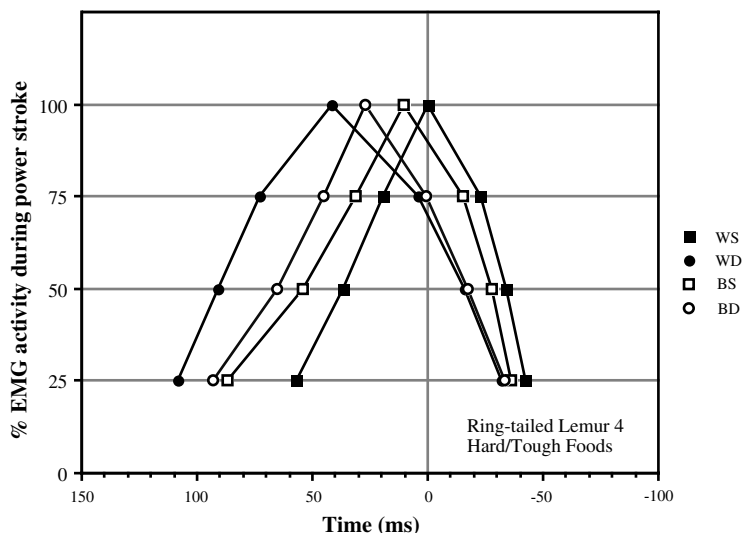


Figure 11.10. Mean values for the timing of average percent EMG activity of the deep and superficial masseters during the chewing of hard/tough foods in lemur 4. Similar to baboons, macaques, and owl monkeys, and unlike thick-tailed galagos, the working-side deep masseter reaches peak activity first. The vertical line indicates peak activity in the reference muscle, which, in contrast to the situation in the above anthropoids, is the last muscle to reach peak activity in ring-tailed lemurs (and thick-tailed galagos). Symbols and abbreviations as in Figure 11.3 (from Hylander *et al.*, 2000).

Discussion

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

The symphyseal fusion–muscle recruitment hypothesis predicts that although anthropoids, galagos, and lemurs recruit about the same percentage of working-side masseter force, and therefore exhibit a similar percentage of working-side masseter EMG activity, anthropoids recruit much more balancing-side muscle force. Therefore, anthropoids should have W/B EMG ratios that are relatively small and similar to one another, whereas the strepsirrhines should have W/B ratios that are relatively large. The data in Table 11.1 and Figure 11.5 support certain aspects of this prediction. For example, all species exhibit 55% 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, and all anthropoids have relatively small W/B ratios. On the other hand, lemurs have an average W/B ratio for the superficial masseter that is actually slightly smaller than for baboons. Moreover, there is extensive overlap of the W/B ratios for the superficial masseter between galagos and anthropoids. For the deep masseter, however, there is no overlap of the W/B ratio values between the strepsirhines and anthropoids. Therefore, the only clear difference in W/B ratios between these strepsirhines 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 is that when the W/B EMG ratios for the deep masseter are small, as in anthropoids, this may not be due to large contributions of force from the balancing-side deep masseter, but instead is due to small contributions of force from the working-side deep masseter. If so, this of course means that both the working-side and balancing-side deep masseters in anthropoids are weakly recruited during forceful mastication. 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 produce bite force and movement during chewing and biting.

Thus, when primates engage in forceful chewing behaviors, small W/B EMG ratios are best interpreted as indicating relatively large contributions of force from the balancing-side masseter, just as large W/B EMG ratios are best interpreted as indicating relatively small contributions of force from the balancing-side masseter. Furthermore, the results of this EMG analysis are similar to the results of our recent analysis of mandibular corpus bone strains during forceful mastication. This analysis demonstrates that although peak working-side corpus strains are rather similar for macaques, galagos, and owl monkeys, the galagos have much smaller peak balancing-side corpus strains than macaques and owl monkeys. Thus, macaques and owl monkeys have small average W/B mandibular strain ratios whereas galagos have large W/B strain ratios, indicating that compared to galagos, anthropoids recruit more balancing-side muscle force during forceful mastication (Hylander *et al.*, 1998).

Finally, although not directly related to whether the masseter muscles are strongly recruited during forceful mastication, we have established that the magnitude of peak masseter EMG is intensely correlated with peak masseter force during the power stroke of mastication (Hylander and Johnson, 1989, 1993). This finding increases the likelihood that our W/B ratio data do indeed provide a good approximation of the recruitment of relative masseter force during mastication.

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.

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 whereas galagos and lemurs do not.

The data in Tables 11.2 and 11.3 indicate quite clearly that the balancing-side deep masseter firing pattern for galagos and lemurs is quite different from that for owl monkeys, macaques, and baboons. Furthermore, the firing pattern for owl monkeys is very similar to the one for baboons and macaques, i.e., in all three anthropoids the last muscle to reach peak activity is the balancing-side deep masseter. Thus, as illustrated in Figures 11.6–11.10, a major difference in firing patterns between the strepsirhines and anthropoids is related to the behavior of the balancing-side 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).

Wishboning and the balancing-side deep masseter

In 1994 we discussed the various external forces associated with wishboning of the macaque mandible during mastication (Hylander and Johnson, 1994). These forces (Fig. 11.11) are the laterally directed component to the bite force (F_b) and the opposite laterally directed component to the balancing-side jaw muscle force (F_{mb}). These two force components are probably not equal as residual force associated with the relaxing working-side jaw adductors (F_{mw}) also 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

¹ The 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

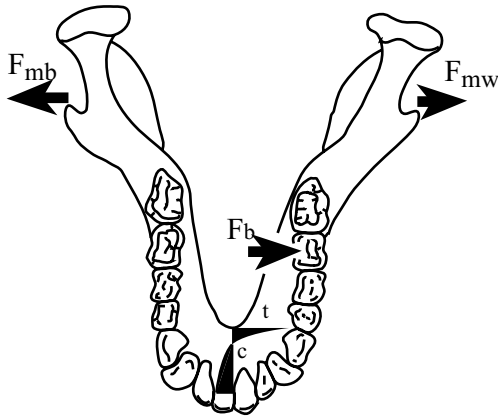


Figure 11.11. Lateral bending or wishboning of the macaque mandibular symphysis. F_b , transverse component to the bite force; F_{mb} , transverse component to the balancing-side jaw-closing muscle force; F_{mw} , transverse component to the working-side jaw-closing muscle force. These three forces wishbone the mandible. The length of the arrows does not indicate the relative magnitude of bite and muscle forces. The darkly shaded areas along the symphysis indicate the distribution of bending stress for a symmetrical curved beam: t , tensile bending stress; c , compressive bending stress. 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).

The EMG data provide strong evidence for the hypothesis that thick-tailed galagos and ring-tailed lemurs do not significantly wishbone their mandibles during mastication. This is because of two main factors. First, galagos and lemurs recruit relatively low levels of force from their balancing-side deep masseter. Whereas the deep masseter W/B ratio is near unity for anthropoids, it is three to four times larger for lemurs and galagos (2.7 to 4.4., respectively). Second, and perhaps most importantly, unlike anthropoids, galagos and lemurs do not exhibit the late firing of the balancing-side deep masseter. That is, they do not have the wishboning firing pattern. Thus, our EMG data strongly support the hypothesis that symphyseal fusion and transversely directed muscle force in anthropoids are functionally linked. These data do not, however, help us to determine whether symphyseal fusion is an adaptation to strengthen the

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 are rapidly decreasing and the balancing-side deep masseter force is rapidly increasing or has peaked (Hylander and Johnson, 1994).

symphysis, or to stiffen the symphysis (Hylander *et al.*, 2000; Lieberman and Crompton, 2000). Recently, however, Hogue and Ravosa (2001) and Vinyard *et al.* (in press b) provide a compelling argument that supports the strengthening hypothesis.

Muscle recruitment and firing of the masseter in strepsirhines

Compared to anthropoids, the W/B ratios for lemurs and galagos demonstrate that these strepsirhines recruit much less relative force from their balancing-side deep masseter. Furthermore, these data also suggest that lemurs recruit relatively more balancing-side deep masseter force than do galagos (deep masseter W/B ratio = 4.4 and 2.4 for galagos and lemurs, respectively). This finding is interesting simply because Beecher's data indicate that although the symphysis of *Lemur catta* is unfused, it is much stiffer and stronger than is the unfused symphysis of *Otolemur crassicaudatus* (Beecher, 1977). This leads us to speculate that the differences in mechanical characteristics of the symphysis of ring-tailed lemurs and thick-tailed galagos are functionally linked to differences in muscle force recruitment patterns. Thus, compared to thick-tailed galagos, perhaps the stiffer and stronger symphysis of ring-tailed lemurs is better able to counter increased balancing-side muscle force during mastication.

There are also some interesting differences between galagos and lemurs in the firing patterns of their deep masseters. Our data indicate that unlike nonhuman anthropoids, galagos and lemurs do not have the late firing pattern of the balancing-side deep masseter (Hylander *et al.*, 2000, 2002). Furthermore, galagos do not have the early firing pattern of the working-side deep masseter (Figs. 11.3 and 11.9) (Hylander *et al.*, 2000). These data initially led Ravosa *et al.* (2000) to speculate that the deep and superficial masseters of strepsirhines are tightly coupled in their firing patterns.

Our data on ring-tailed lemurs, however, demonstrate conclusively that the firing patterns of superficial and deep masseters in strepsirhines are uncoupled. In ring-tailed lemurs the working-side deep and superficial masseters do not fire simultaneously as the working-side deep masseter reaches peak activity very early during jaw closing, and the working-side superficial masseter reaches peak activity late in the power stroke (Hylander *et al.*, 2002). Moreover, in lemurs the balancing-side deep and superficial masseters also do not fire simultaneously as the balancing-side deep masseter reaches peak activity early during jaw closing, well before the balancing-side superficial. Finally, recent work on sifakas demonstrates that the superficial and deep masseters also fire asynchronously on both the working and balancing sides during mastication (Hylander *et al.*, 2003).

Conclusions

The functional morphology of the craniofacial region of primates continues to attract a significant amount of research interest. One problem that has received a considerable amount of attention is related to the adaptive significance of symphyseal fusion in mammals. This is a particularly interesting problem as symphyseal fusion has evolved independently in many different mammalian lineages. In spite of many morphological and comparative studies, there is little agreement as to the ultimate reasons for symphyseal fusion. Therefore, we have focused our research on the more immediate or proximate factors that can be plausibly linked to the evolution of symphyseal fusion, and thus to determine if certain types of biomechanical situations or loading patterns are associated with symphyseal fusion.

In this study we tested several hypotheses about how balancing-side jaw-adductor muscles are recruited in primates, and in turn are possibly linked to symphyseal fusion. These hypotheses predict that anthropoids have W/B EMG ratios that are relatively small and similar to one another, and strepsirrhines have W/B ratios that are relatively large.

Our data indicate that galagos have the largest W/B ratios for both the superficial and deep masseters, and anthropoids have relatively small W/B ratios. On the other hand, lemurs have W/B ratios for the superficial masseter that are actually smaller than those for baboons, although their W/B ratios for the deep masseter are relatively large. Thus, the only sharp distinction in W/B EMG ratios between thick-tailed galagos and ring-tailed lemurs as compared to anthropoids is associated with the deep masseter. That is, during mastication the balancing-side deep masseter of anthropoids is much more active than is the balancing-side deep masseter of thick-tailed galagos and ring-tailed lemurs. Furthermore, the analysis of masseter firing patterns indicates that whereas baboons, macaques, and owl monkeys possess the deep masseter wishboning firing pattern, galagos and lemurs do not. Thus, the W/B ratios and firing patterns of the deep masseter support the hypothesis that symphyseal fusion and transversely directed muscle force are functionally linked in anthropoids.

Acknowledgments

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