

Electromyography of the Anterior Temporalis and Masseter Muscles of Owl Monkeys (*Aotus trivirgatus*) and the Function of the Postorbital Septum

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ABSTRACT Anthropoids and tarsiers are distinguished from all other vertebrates by the possession of a postorbital septum, which is formed by the frontal, alisphenoid, and zygomatic bones. Cartmill [(1980) In: *Evolutionary Biology of the New World Monkeys and Continental Drift*. New York: Plenum, p 243–274] suggested that the postorbital septum evolved in the stem lineage of tarsiers and anthropoids to insulate the eye from movements arising in the temporal fossa. Ross [(1996) *Am J Phys Anthropol* 91:305–324] suggested that the septum insulates the orbital contents from incursions by the line of action of the anterior temporal muscles caused by the unique combination of high degrees of orbital frontation and convergence. Both of these hypotheses must explain why insulation of the orbital contents could not be achieved by decreasing the size of the anterior temporal musculature with a corresponding increase in size of the remaining jaw adductors, rather than evolving a postorbital septum. One possibility is that the anterior temporalis is an important contributor to vertically directed bite forces during all biting and chewing activities. Another possibility is that reduction in anterior temporal musculature would compromise the ability to produce powerful bite forces, either at the incisors or along the postcanine toothrow. To evaluate these hypotheses, electromyographic (EMG) recordings were made from the masseter muscle and the anterior and posterior portions of the temporalis muscles of two owl monkeys, *Aotus trivirgatus*. The EMG data indicate that anterior temporalis activity relative to that of the superficial masseter is lower during incision than mastication. In addition, activity of the anterior temporalis is not consistently higher than the posterior temporalis during incision. The data indicate relatively greater activity of anterior temporalis compared to other muscles during isometric biting on the postcanine toothrow. This may be due to decreased activity in superficial masseter and posterior temporalis, rather than elevated anterior temporalis activity. The anterior temporalis is not consistently less variable in activity than the

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superficial masseter and posterior temporalis. The EMG data gathered here indicate no reason for suggesting that the anterior temporal muscles in anthropoids are utilized especially for incisal preparation of hard fruits. Maintenance of relatively high EMG activity in anterior temporalis across a wide range of biting behaviors is to be expected in a vertically oriented and rostrally positioned muscle such as this because, compared to the posterior temporalis, superficial masseter and medial pterygoid, it can contribute relatively larger vertical components of force to bites along the postcanine toothrow. The *in vivo* data do not support this hypothesis, possibly because of effects of bite point and bite force orientation. *Am J Phys Anthropol* 112: 455–468, 2000. © 2000 Wiley-Liss, Inc.

Anthropoids and tarsiers are distinguished from all other vertebrates by the possession of a postorbital septum, which is formed by the frontal, alisphenoid, and zygomatic bones. The restricted distribution and distinctiveness of the postorbital septum have ensured that hypotheses regarding its function have featured prominently in adaptive explanations for anthropoid or haplorhine origins (Cachel, 1979; Cartmill, 1970, 1972, 1980; Ross, 1993, 1994, 1995a, b, 1996; Ross and Hylander, 1996). There are currently two viable hypotheses regarding the original function of the postorbital septum.

Cartmill (1980) suggested that the postorbital septum evolved in the stem lineage of tarsiers and anthropoids to insulate the eye (sensitized to nonconjugate eye movements by the evolution of a retinal fovea) from masticatory movements in the temporal fossa. More recently, it has been suggested that even in the absence of a fovea the postorbital septum might have evolved to protect the orbital contents from incursions by the anterior temporal muscles because of increased orbital frontation and convergence (Ross, 1992; 1994; 1995a,b). Ross (1996) argued that this increased frontation and convergence probably evolved, along with a postorbital septum, in conjunction with a shift to diurnality at small body size (<1300 g).

Both of these “insulation” hypotheses imply that disturbance of the orbital contents was most easily avoided by evolving a postorbital septum and not by decreasing the size of the anterior temporal musculature. Strepsirrhine primates lack a postorbital septum, and many small strepsirrhines

have reduced amounts of temporal musculature between the temporalis tendon and the periorbital (Ross, 1995b). If small strepsirrhines can adopt such a strategy for separating the contents of the orbit and temporal fossa, why did the haplorhine stem lineage not also reduce the size of its anterior temporal muscles? Here we evaluate three hypotheses regarding the function(s) of the anterior temporal musculature in a small haplorhine in an attempt to answer these questions (Fig.1).

CATHOLIC RECRUITMENT HYPOTHESIS

The anatomy of the haplorhine anterior temporal muscles — characterized by the longest lever arm and most vertical orientation of any of the masticatory muscles (Ross, 1995b) — makes them useful for generation of vertically directed components of bite force during many activities. If this is the case, reduction in the size of the anterior temporal musculature would be selected against because it would compromise the overall ability of the masticatory muscles to produce powerful forces during many activities, including incision, postcanine biting, and the power stroke of mastication.

However, according to this line of reasoning, vertically oriented and anteriorly positioned temporal muscles would also be useful to small strepsirrhines, yet small strepsirrhines have small anterior temporal muscles. Moreover, all other things being equal, muscle cross-sectional area will scale with negative allometry relative to body mass, meaning that small-bodied animals are actually less likely to need large anterior temporal muscles than large-bodied an-

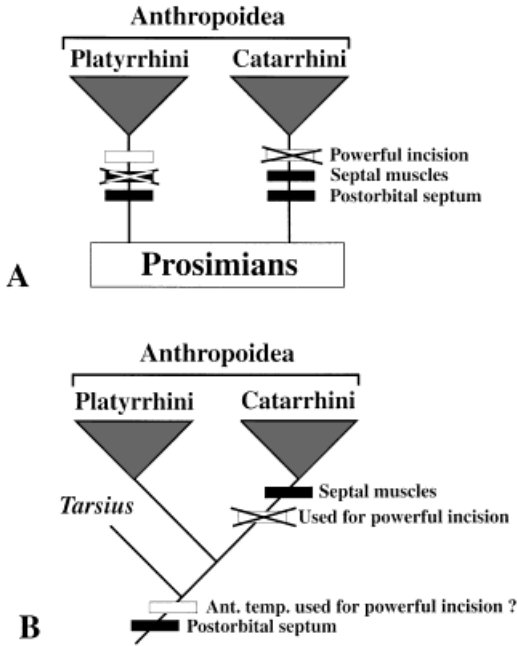


Fig. 1. Cladograms illustrating two hypothesized relationships of anthropoids and patterns of character state evolution. (A) Pattern of relationships and character state evolution hypothesized by Cachel (1979). The two major groups of anthropoids are argued to have evolved independently from separate prosimian (non-anthropoid) ancestors. In both lineages, the evolution of the postorbital septum, muscle attachment to the septum, and powerful incision utilizing septal muscle fibers are hypothesized to have evolved together. The large crosses over hypothesized character states illustrate Ross' (1995b) demonstration that muscles do not attach to most of the postorbital septum in platyrrhines; and Hylander and Johnson's (1985) demonstration that septal muscle fibers are not utilized more than other muscles for powerful incision in catarrhines. (B) Working hypothesis of relationships and character state evolution used in this study. Anthropoidea (Platyrrhini + Catarrhini) is monophyletic and tarsiers constitute their sister taxon. The postorbital septum evolved once and septal muscle attachments evolved later in the stem lineage of catarrhines (Ross, 1995b.). These septal muscle fibers were probably not used more than other muscles for powerful incision in the catarrhine stem lineage (Hylander and Johnson, 1985). The hypotheses under test pertain to the function of the anterior temporalis muscle fibers in the earliest anthropoids.

imals. And, indeed, large fleshy anterior temporal muscle bellies are only found rostral to the temporalis tendon in large species such as *Indri indri* and *Propithecus verreauxi*, while among haplorhines, extensive origin of anterior temporal muscle fibers from the postorbital septum is characteristic of large taxa such as many *Papio anubis*,

Aouatta caraya, and *Pongo pygmaeus* (Ross, 1995b). If the small stem haplorhines did indeed need to retain large anterior temporal muscles, it must have been in relation to a function not performed by extant small strepsirrhines.

INCISOR BITING HYPOTHESIS

One of the most obvious differences between strepsirrhines and haplorhines is related to the anterior dentition. Strepsirrhines have a toothcomb made up of comparatively gracile and procumbent lower incisors, whereas haplorhines have more robust, vertically oriented incisors. This difference led Cachel (1979) to propose that the postorbital septum of anthropoids evolved (in parallel in catarrhines and platyrrhines) to augment the available attachment area for anterior temporalis muscles and that the additional anterior temporalis increased vertically directed incisor bite forces used for incisal preparation of large and obdurate fruits.

Cachel's (1979) hypothesis is falsified by both the anatomy of the primate anterior temporal fossa (Ross, 1995b) and patterns of muscle activity in the macaque and human anterior temporalis and masseter muscles (Hylander and Johnson, 1985). Soft tissue anatomy of extant haplorhines and the bony morphology of the oldest known haplorhine postorbital septum, that of *Catopithecus browni*, suggest that stem haplorhines probably lacked extensive origins for anterior temporal muscles on the postorbital septum (Ross, 1995b) (Fig. 1). Moreover, patterns of masticatory muscle activity recorded from macaque monkeys indicate that the muscle fibers attaching to the postorbital septum are not more active than masseter during incision as Cachel's hypothesis predicts; nor are they more active during incision than during mastication (Hylander and Johnson, 1985). Together, these anatomical and functional data suggest that the septum evolved before muscles migrated onto it and when muscle origins did spread to the septum, this was not necessarily part of an adaptation for powerful incisor biting (Fig. 1).

Paradoxically, although the anatomical and EMG data falsify the "muscle attachment" hypothesis presented by Cachel, the

anatomical data also suggest that early anthropoids resembled most platyrrhines in having a very small amount of anterior temporalis muscle attaching to the postorbital septum, not the extensive attachment of zygomatico-mandibularis and anterior temporalis seen in macaques (Ross, 1995b). Nevertheless, hypotheses regarding muscle function in early anthropoids are better evaluated using a small platyrrhine. Therefore, although Cachel's (1979) hypothesis has been falsified, a new hypothesis is worth evaluating: that the anterior temporal muscles of small haplorhines are utilized for powerful incisor biting. Corroboration of this hypothesis would suggest that the postorbital septum evolved in stem haplorhines not to augment the attachment area for anterior temporal muscles, but to enable the muscles already there to maintain their size and their importance for incisor biting.

POSTCANINE BITING

Cachel's (1979) work focused attention on the relationship between anterior temporal muscle function and biting on the anterior tooththrow. Little work has been done on the possibility that the anterior temporal muscles are important for powerful biting along the postcanine tooththrow. Muscle activity during unilateral isometric biting is expected to be affected by the position of the bite point for theoretical reasons (Greaves, 1978; Spencer, 1995), an expectation that is confirmed by experimental data (Pruim et al., 1980; Spencer, 1998). Here we evaluate the hypothesis that the anterior temporalis might be important for powerful isometric biting on the postcanine tooththrow.

The first hypothesis, the catholic recruitment hypothesis, predicts that although the anterior temporalis need not be consistently more active than other muscles during any one specific behavior, it should show a comparatively consistent level of activity over a wide range of chewing and biting behaviors. The second, the incisor biting hypothesis, predicts greater activity of anterior temporalis relative to masseter and posterior temporalis during incision, and relatively greater activity of anterior temporalis during incision than during mastication or postcanine biting. The third hypothesis, the

postcanine biting hypothesis, predicts greater activity of the anterior temporalis relative to masseter and posterior temporalis during biting along the ipsilateral postcanine tooththrow, and relatively greater activity of anterior temporalis during ipsilateral postcanine biting than during mastication or incision.

In order to evaluate these three hypotheses, muscle activity was measured in the masseter and anterior and posterior temporalis muscles during mastication, incision, and isometric biting along the postcanine tooththrow in two owl monkeys (*Aotus trivirgatus*). Although *Aotus* differs from the putative stem haplorhines in being nocturnal (Ross, 1996), the anatomy of its anterior temporal muscles closely matches that of small diurnal anthropoids, suggesting that it is an appropriate model with which to evaluate these hypotheses.

MATERIALS AND METHODS

Subjects

Two adult owl monkeys (*Aotus trivirgatus*), one male and one female, served as subjects. Both initially had a full complement of teeth with normal occlusion; however, sometime during the one month interval between experiments 8 and 9, owl monkey 2 broke off the left canine below the cervical portion of the crown, in circumstances unknown to us. The gingival tissue healed completely and comparisons of data recorded during experiments 8 and 9 reveal no obvious behavioral differences.

EMG Electrodes: Design and Placement

The EMG data were gathered using indwelling bipolar fine-wire electrodes following procedures outlined in Hylander and Johnson (1985). Following sedation with ketamine hydrochloride and acepromazine (Connolly and Quimby, 1978), the electrodes were placed in the muscles percutaneously. To do this, the exposed tips of the two wires were inserted into the sharp end of a 25-gauge hypodermic needle and the wires bent to lie along the shaft of the needle. This created small hooks in the ends of the wires. The needle was then inserted into one of the jaw muscles until it contacted bone. The

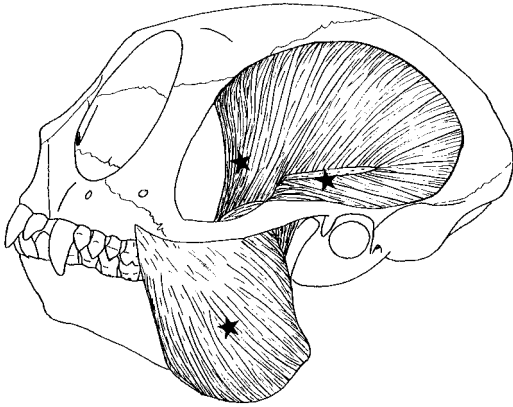


Fig. 2. Lateral view of *Aotus* head illustrating general surface anatomy of the temporalis and masseter muscles. Stars indicate positions of electrode placement as described in the text.

needle was then withdrawn while gently holding the wires against the skin with a pair of needle-nosed forceps. The electrodes were then placed in a 19-pin Amphenol Connector (series 222) which was taped securely to the back of the subject's neck.

In five experiments, electrodes were placed bilaterally in the anterior-most temporalis muscle fibers arising from the frontal portion of the postorbital septum (see Fig. 2 for electrode positions). This was done by inserting the needle into the anterior temporalis muscle at an anteromedial and slightly inferior angle until it contacted the postorbital septum. Electrodes were also placed bilaterally in the posterior temporalis immediately anterior to the tragus of the ear, and bilaterally in the central portion of each superficial masseter.

EMG Recording Procedure

The subjects were restrained in a cat restraint system made to our specifications by Alice King Medical Arts Ltd., Hawthorne CA. This restraint consists of a sling suit suspended from two horizontal metal bars. The monkey's legs, arms, and tail were taped to the posts supporting the restraining apparatus, leaving the head and neck to move freely.

The Amphenol Connector was connected via leads to Grass P511J differential pre-amplifiers where the EMG potentials were

simultaneously amplified (200–10,000 \times) and band-pass filtered (100–3,000 Hz). The EMG potentials were recorded on a 14-channel FM tape recorder (Bell and Howell Datatape 4020A) at 15inch/sec.

The owl monkeys were fed dried apricots, dried prunes, prune stones with flesh attached, and gelatin candies ("gummy bears"). The foods were held firmly and motionless in front of the animal with a pair of forceps so that the animal bit on them with its incisors and EMG potentials were recorded. EMG activity was continuously recorded while the subject chewed the food. The side on which chewing took place was noted on the voice track of the tape recorder. At the end of each recording session, the animal was again sedated, the electrodes were removed, and the monkey returned to its cage.

EMG Data Analysis

The raw EMG recordings were played out on a six-channel chart recorder (Brush 260, Gould Inc., Cleveland Ohio, USA) and visually examined in order to identify movement artifacts. For selected sequences, the EMG potentials were full-wave rectified, passed through a low-pass RC filter (40 msec time constant) and played out on the chart recorder. This so-called averaged EMG is an appropriate measure of muscle activity to use because it has been shown to be highly correlated with muscle force under isometric conditions (e.g., Møller, 1966; Ahlgren, 1966; Luschei and Goodwin, 1974; Hylander and Johnson, 1985, 1989), and the hypotheses under consideration specify powerful biting or the power stroke of powerful mastication, which occur under near isometric conditions. The maximum amplitudes of the averaged EMG recorded from the anterior temporalis, posterior temporalis, and superficial masseter during each mastication and incision power stroke were determined directly from the chart recording. Following Hylander and Johnson (1985), the EMG values recorded from each electrode were then standardized by assigning a value of 1.0 to the highest mastication value recorded from that electrode. The remaining mastication and incision values were then scaled in a linear fashion.

Statistical Analyses

The three hypotheses presented above suggest that the anterior temporalis muscles of platyrrhines function for the generation of powerful bite forces during (1) all powerful biting and mastication activities, (2) incisal preparation of food objects, and (3) isometric biting along the postcanine tooththrow. Hypothesis 1, the catholic recruitment hypothesis, is corroborated if hypotheses 2 and 3 are falsified and if the anterior temporalis shows less variable levels of activity than the other muscles over all activities. Hypothesis 2, the incisal biting hypothesis, is corroborated if the anterior temporalis is absolutely, and relative to all other masticatory muscles, more active during incision than postcanine biting or mastication. Hypothesis 3, the postcanine biting hypothesis, is corroborated if the anterior temporalis is absolutely, and relative to all other masticatory muscles, more active during postcanine biting than incision or mastication.

Hypothesis 1 was evaluated by comparing the variance in anterior temporalis activity with activity in superficial masseter and posterior temporalis. These comparisons were made across all behaviors. Variances were compared using an *F*-test for homogeneity of variances. Following Hylander and Johnson (1985), the predictions of hypotheses 2 and 3 were tested by calculating and comparing the ratio of the averaged EMG activity recorded in the superficial masseter over the averaged EMG activity recorded in the anterior temporalis (SMASS/ATEMP) for incision, biting on the postcanine tooththrow, and mastication. Similarly, the ratios of averaged EMG activity recorded in the posterior temporalis relative to EMG activity recorded in anterior temporalis (PTEMP/ATEMP) during incision, postcanine biting and mastication were compared. The comparisons were carried out using unpaired one-tailed *t*-tests or, when the data were skewed and/or heteroscedastic, using a nonparametric Mann-Whitney *U*-test.

The predictions were also evaluated by plotting averaged EMG activity recorded from the posterior temporalis or superficial masseter (*x*-axis) and the anterior tempora-

lis (*y*-axis) on each side during each experiment. The reduced major-axis regression line for the working-side mastication values were added to each plot, and different symbols were used to indicate EMG values recorded during mastication, incision, and biting on the postcanine tooththrow. These plots allowed visual comparison of the relative magnitudes of activity in, for example, superficial masseter and anterior temporalis on each side during mastication, incision, and biting along the postcanine tooththrow. If during incision the anterior temporalis is more active relative to the masseter than during mastication, the values recorded during incision will lie above the regression line for the mastication values. Conversely, if the masseter is more active relative to the anterior temporalis, the values recorded during incision will lie below the regression line for the mastication values.

RESULTS

Six separate experiments were performed on the two owl monkeys. In four experiments [experiments 3 and 7 on owl monkey 1 (male) and experiments 8 and 9 on owl monkey 2 (female)] all electrodes functioned properly. In two experiments (experiments 1 and 4 on owl monkey 1), the electrodes in the right anterior temporalis malfunctioned so the only data analyzed from these experiments were those recorded from the left-side muscles. From each of these experiments, sequences of mastication and incision of dried apricot, dried prune, and dry gelatin candy ("gummy bears") were chosen for analysis because these foods elicit relatively high levels of EMG activity, allowing us to test predictions of the hypotheses regarding muscle function during incision and mastication of hard food objects.

Catholic Recruitment Hypothesis

The variances for the EMG amplitudes recorded from the superficial masseter, anterior temporalis, and posterior temporalis during the six experiments examined here are given in Table 1. The hypothesis that the anterior temporalis shows less variability in activity level than the other two muscles is tested using *F*-test comparisons of variances. Of the 20 possible comparisons,

TABLE 1. Variances for and results of *f*-test comparisons of variances

	Left side		Right side	
	<i>n</i>	Variance (<i>P</i>) ¹	<i>n</i>	Variance (<i>P</i>) ¹
Owl monkey 1				
Experiment 1	103			
ATEMP		.052		
PTEMP		.048 ns		
SMASS		.052 ns		
Experiment 3	225		225	
ATEMP		.047		.062
PTEMP		.063 (.0117)		.052 ns
SMASS		.021 ns	.068 ns	
Experiment 4	396			
ATEMP		.054		
PTEMP		.058 ns		
SMASS		.046 ns		
Experiment 7	307		307	
ATEMP		.042		.034
PTEMP		.045 ns		.048 (.0007)
SMASS		.045 ns		.030 ns
Owl Monkey 2				
Experiment 8	436		436	
ATEMP		.039		.066
PTEMP		.053 (.001)		.056 ns
SMASS		.053 (.001)		.053 ns
Experiment 9	211		211	
ATEMP		.028		.036
PTEMP		.034 ns		.040 ns
SMASS		.019 ns		.037 ns

¹ *P*-values are given for unpaired one-tailed *F*-tests corroborating the hypothesis that the variance in ATEMP activity is less than that in PTEMP or SMASS. ns = ATEMP variance not significantly smaller than PTEMP or SMASS. *n* = number of power strokes or bites.

only four revealed that the anterior temporalis was significantly less variable than the superficial masseter or posterior temporalis.

Incisor Biting Hypothesis

The descriptive statistics for SMASS/ATEMP EMG ratios and the results of the unpaired comparisons between the ratios are given in Table 2 (left side muscles) and Table 3 (right side muscles). The descriptive statistics for PTEMP/ATEMP ratios and the results of the unpaired comparisons between the ratios are given in Table 4 (left side muscles) and Table 5 (right side muscles). A summary of these results is given in Table 6.

Of the ten comparisons of SMASS/ATEMP ratios recorded during mastication with those recorded during incision, four indicate no significant differences between these ratios (Tables 2 and 3). Figure 3 is a bivariate plot illustrating one set of data that gave this result: EMG amplitudes re-

corded from the left superficial masseter and left anterior temporalis during experiment 3. Note that the values recorded during incision fall among those recorded during left-sided chewing. It is also noteworthy that at higher EMG amplitudes, all incision values fall below the regression line, suggesting more activity in superficial masseter than anterior temporalis. Stronger support for this result comes from four out of ten comparisons of SMASS/ATEMP, indicating relatively greater activity in the superficial masseter during incision than during mastication (Table 2). Figure 4 illustrates one set of data that yields this result: EMG amplitudes recorded from the left superficial masseter and left anterior temporalis during experiment 4. Note that the majority of the incision values fall below the reduced major-axis regression line for the ipsilateral mastication values. Of the ten comparisons of SMASS/ATEMP ratios recorded during mastication with those recorded during incision, only two indicate relatively greater activity in the anterior temporalis during incision (Table 2). Figure 5 is a bivariate plot of one set of data which yielded this result: EMG amplitudes recorded from the left superficial masseter and left anterior temporalis during experiment 7.

Ten comparisons were made between PTEMP/ATEMP ratios recorded during incision with ratios recorded during mastication (Tables 4 and 5). Four of these comparisons reveal that the posterior temporalis was more active than the anterior temporalis during incision; two comparisons reveal that the anterior temporalis was more active; and four comparisons reveal no significant differences.

In sum, only four comparisons out of a total of 30 support the hypothesis that anterior temporalis is more important for incision than for mastication, or that it is more important for incision than the superficial masseter or posterior temporalis (Table 6).

Postcanine Biting Hypothesis

Powerful biting along the postcanine tooththrow was successfully elicited in six experiments. In experiment 9, only two postca-

TABLE 2. Descriptive statistics and results of unpaired comparisons of left mass/atemp ratios

	Statistic				Comparisons ¹		
	<i>n</i>	Mean	<i>s</i>	Range	Mastication	Incision	Postcanine
Owl monkey 1							
Experiment 1							
Mastication	24	1.40	.51	.78–2.54	*	.0086	
Incision	21	.99	.22	.35–1.31	<i>Z</i> = -2.628 (I-)	*	
Experiment 3							
Mastication	116	1.31	.78	0.48–5.22	*	ns	
Incision	49	1.21	.39	0.74–2.73	ns	*	
Experiment 4							
Mastication	84	.97	.14	0.63–1.41	*	.0074	.0003
Incision	75	1.03	.15	0.74–1.48	<i>t</i> = 2.462 (I+)	*	<.0001
Postcanine biting	58	.89	.12	0.67–1.31	<i>t</i> = 3.544 (P-)	<i>t</i> = 5.777 (P-)	*
Experiment 7							
Mastication	126	1.01	.37	0.38–3.36	*	<.0001	<.0001
Incision	65	.71	.25	0.37–1.54	<i>Z</i> = -6.394 (I-)	*	ns
Postcanine biting	14	.63	.12	0.49–0.83	<i>Z</i> = -4.583 (P-)	ns	*
Owl Monkey 2							
Experiment 8							
Mastication	141	1.18	.31	.39–3.19	*	ns	<.0001
Incision	110	1.19	.39	.59–4.25	ns	*	<.0001
Postcanine biting	14	.90	.15	.63–1.13	<i>Z</i> = -4.304 (P-)	<i>Z</i> = -4.074 (P-)	*
Experiment 9							
Mastication	75	.96	.14	.49–1.39	*	.0019	
Incision	50	1.06	.20	.73–1.10	<i>t</i> = 3.179 (I+)	*	
Postcanine biting	2			.87&1.10			

¹ For each significant comparison, the *t*-value or *Z*-value is given below the diagonal (asterisks), and *P* is given above the diagonal. ns = no significant difference between ratios; *n* = number of power strokes or bites; *s* = standard deviation.

TABLE 3. Descriptive statistics and results of unpaired comparisons of right mass/atemp ratios

	Statistics				Comparisons ¹		
	<i>n</i>	Mean	<i>s</i>	Range	Mastication	Incision	Postcanine
Owl monkey 1							
Experiment 3							
Mastication	48	1.04	.20	.38–1.49	*	ns	ns
Incision	49	1.04	.23	.60–1.73	ns	*	ns
Postcanine biting	8	1.08	.11	.98–1.33	ns	ns	*
Experiment 7							
Mastication	82	1.99	1.38	.56–9.09	*	ns	ns
Incision	46	1.89	.50	1.23–3.31	ns	*	ns
Postcanine biting	20	1.46	.38	.66–1.95	ns	ns	*
Owl Monkey 2							
Experiment 8							
Mastication	159	1.07	.23	.41–2.70	*	<.0001	
Incision	110	1.89	1.04	.61–6.38	<i>Z</i> = -9.591 (I+)	*	
Experiment 9							
Mastication	80	1.35	.40	.72–4.19		.0014	
Incision	50	1.69	1.18	1.10–9.14	<i>Z</i> = -3.192 (I+)	*	

¹ For each significant comparison, the *t*-value or *Z*-value is given below the diagonal (asterisks), and *P* is given above the diagonal. ns = no significant difference between ratios; *n* = number of power strokes or bites; *s* = standard deviation.

nine bites were elicited during the sequences examined; thus no statistical comparisons were possible. Therefore, it was possible to make only five comparison of ratios recorded during biting on the postcanine tooththrow with those recorded during mastication or incision.

Of the five comparisons of SMASS/ATEMP ratios recorded during biting on the postcanine tooththrow with those recorded

during mastication, two were not significant (Table 3) and three indicated relatively greater activity of the anterior temporalis during biting on the postcanine tooththrow. Five comparisons of SMASS/ATEMP ratios recorded during biting on the postcanine tooththrow with those recorded during incision revealed three that were not significant (e.g., Fig. 3) and two indicating greater activity of the anterior temporalis during

TABLE 4. Descriptive statistics and results of unpaired comparisons of left ptemp/atemp ratios

	Statistics				Comparisons ¹		
	n	Mean	s	Range	Mastication	Incision	Postcanine
Owl monkey 1							
Experiment 1							
Mastication	17	.60	.24	.32–1.18	*	ns	
Incision	21	.67	.17	.43–1.13	ns	*	
Experiment 3							
Mastication	116	1.35	.62	.63–5.12	*	.0003	
Incision	49	1.50	.35	.79–2.68	Z = -3.638 (I+)	*	
Experiment 4							
Mastication	84	.71	.26	.06–1.16	*	ns	<.0001
Incision	75	.63	.22	.13–1.05	ns	*	.0001
Postcanine biting	58	.47	.25	.10–1.03	t = 5.336 (P-)	t = 3.929 (P-)	*
Experiment 7							
Mastication	126	1.09	.25	.36–2.66	*	<.0001	<.0001
Incision	65	.96	.33	.64–3.29	Z = -5.681 (I-)	*	ns
Postcanine biting	14	.91	.12	.70–1.12	Z = -3.923 (P-)	ns	*
Owl Monkey 2							
Experiment 8							
Mastication	141	1.18	.31	.39–3.19	*	ns	ns
Incision	110	1.19	.39	.59–4.25	ns	*	ns
Postcanine biting	14	.86	.13	.59–1.05	ns	ns	*
Experiment 9							
Mastication	79	.69	.17	.26–1.12	*	<.0001	ns
Incision	50	.55	.14	.20–.79	t = -5.023 (I-)	*	ns
Postcanine biting	2			.32 & .60	ns	ns	*

¹ For each significant comparison, the *t*-value or *Z*-value is given below the diagonal (asterisks), and *P* is given above the diagonal. ns = no significant difference between ratios; *n* = number of power strokes or bites; *s* = standard deviation.

TABLE 5. Descriptive statistics and results of unpaired comparisons of right ptemp/atemp ratios

	Statistics				Comparisons ¹		
	n	Mean	s	Range	Mastication	Incision	Postcanine
Owl monkey 1							
Experiment 3							
Mastication	48	1.10	.165	.76–1.76	*	<.0001	ns
Incision	49	1.35	.333	.92–2.58	Z = -5.058 (I+)	*	<.0001
Postcanine biting	8	1.01	.066	.94–1.11	ns	Z = -4.170 (P-)	*
Experiment 7							
Mastication	82	1.96	.768	.25–4.05	*	.0162	.0141
Incision	46	2.26	.525	1.43–4.05	Z = -2.404 (I+)	*	.0016
Postcanine biting	20	1.53	.535	.87–2.80	t = 2.497 (P-)	t = 3.271 (P-)	*
Owl Monkey 2							
Experiment 8							
Mastication	159	1.10	.143	.90–2.09	*	<.0001	
Incision	110	1.44	.412	.95–2.79	Z = -8.501 (I+)	*	
Experiment 9							
Mastication	80	.92	.149	.53–1.38	*	ns	
Incision	50	.94	.308	.58–2.13	ns	*	

¹ For each significant comparison, the *t*-value or *Z*-value is given below the diagonal (asterisks), and *P* is given above the diagonal. ns = no significant difference between ratios; *n* = number of power strokes or bites; *s* = standard deviation.

biting on the postcanine tooththrow (Figs. 4 and 5).

Of the five comparisons of PTEMP/ATEMP ratios recorded during biting on the postcanine tooththrow with those recorded during mastication, two were not significant (Table 3) and three indicated relatively greater activity of the anterior temporalis during biting on the postcanine tooththrow. Of the five comparisons of PTEMP/ATEMP ra-

TABLE 6. Number of comparisons in tables 2–5 which support or falsify hypothesis 2

	Support hypothesis 2		Falsify hypothesis 2	
	ATEMP higher during incision	ATEMP lower during incision	ATEMP higher during incision	No difference
SMASS/ATEMP	2	6	7	7
PTEMP/ATEMP	2	7	6	6

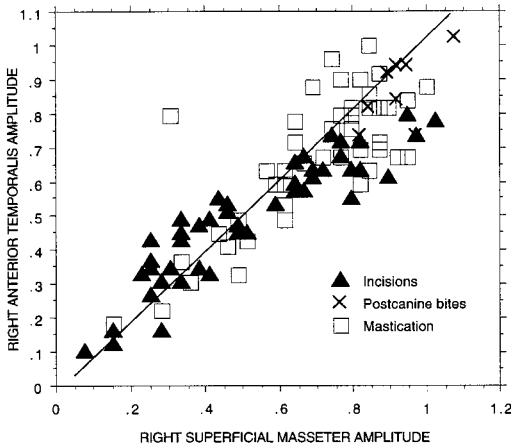


Fig. 3. Plot of peak EMG values recorded from the right superficial masseter and anterior temporalis during the power stroke of incision, mastication, and isometric postcanine biting of dried prune and dried apricot (experiment 3, owl monkey 1). The mastication and isometric biting values consist only of those values recorded during ipsilateral (working-side) power strokes. The reduced major axis for the mastication values is shown ($y = 0.988x - 0.011$, $r = 0.773$).

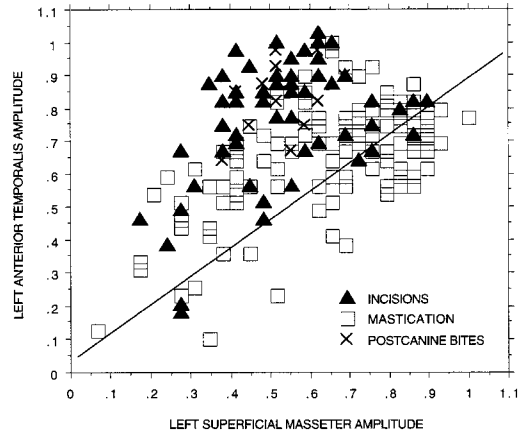


Fig. 5. Plot of peak EMG values recorded from the left anterior temporalis and superficial masseter muscles during the power strokes of mastication and incision, and isometric biting on the postcanine toothrow (experiment 7, owl monkey 1). The foods eaten by the animal were dried prune and dried apricot. Isometric biting was on dried prune and prune stone. The mastication and isometric biting values consist only of those values recorded during ipsilateral power strokes. The reduced major-axis regression line for the mastication values is shown ($y = 0.820 + 0.076x$, $r = 0.544$).

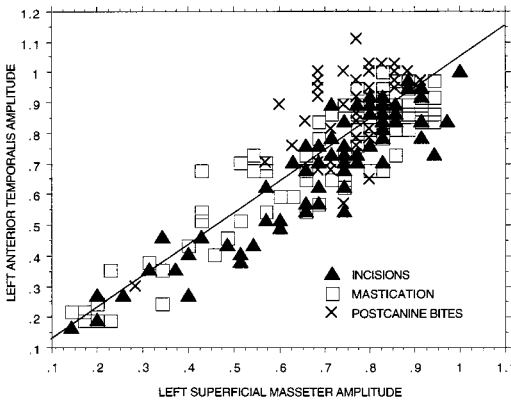


Fig. 4. Plot of peak EMG values recorded from the left anterior temporalis and superficial masseter during the power stroke of mastication on the left side, incision, and left postcanine biting of dried apricot and dried prune (experiment 4, owl monkey 1). The mastication and isometric biting data consist only of those values recorded during ipsilateral power strokes. The reduced major-axis regression line for the mastication values is shown ($y = .994x + 0.026$, $r = 0.922$).

tios recorded during biting on the postcanine toothrow with those recorded during incision, two were not significant (Table 3), and three indicated relatively greater activity of the anterior temporalis during biting on the postcanine toothrow.

DISCUSSION

Data were recorded from the masticatory muscles of owl monkeys in order to evaluate hypotheses that the postorbital septum evolved to insulate the orbital contents from movements associated with the anterior temporal muscles. Three activity groupings were examined: (1) all biting and chewing activities, (2) powerful incision, and (3) powerful unilateral biting on the postcanine toothrow. The working hypothesis in this study is that the evolution of the postorbital septum did not initially involve expansion of muscle attachment areas on its posterior surface, and therefore the earliest anthropoids resembled most extant platyrrhines in having a postorbital septum largely free of muscle attachment. If this hypothesis is correct, EMG data from platyrrhines such as owl monkeys are most appropriate for evaluating hypotheses regarding anterior temporalis muscle function in early anthropoids.

Catholic Recruitment Hypothesis

Being vertically oriented and furthest from the jaw joint, the anthropoid anterior

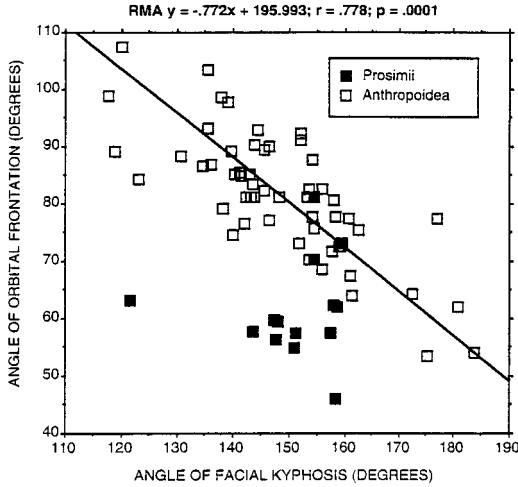


Fig. 6. Plot of the angle of facial kyphosis (AFK) against the angle of orbital frontation. AFK is measured as in Ross and Ravosa (1993). A decrease in AFK reflects a ventral deflection of the palate and an increase in orbital frontation reflects increasing verticality of the orbital margins. Anthropoids have more frontated or vertical orbits than prosimians of equivalent AFK. The RMA line for anthropoids is indicated. This relationship is not significant across prosimians or strepsirrhines.

temporalis muscle has the longest lever arm among the jaw adductors, and it is highly recruited during mastication, incision, and isometric biting. Furthermore, owl monkey anterior temporal muscle fibers are more vertically oriented than the masseter and posterior temporalis fibers (see Fig. 2). Gaspard (1972) inferred from dissections that, compared with prosimians, this is generally true for all anthropoids. Observations on muscle fiber orientation in various primates corroborate this hypothesis (Ross, 1995b).

Morphometric data also suggest that anthropoids have more vertically oriented anterior temporal muscles than most prosimians (Ross and Ravosa, 1993; Ross, 1995). Anthropoids have more frontated or vertically oriented orbits at a given angle of facial kyphosis (AFK) than most prosimians, as illustrated by Figure 6. In this figure, the angle of orbital frontation is plotted against the AFK (Ross and Ravosa, 1993), and increased angle of orbital frontation relative to a nasion-inion chord is associated with increased verticality of the orbital margin relative to the palate. Because anterior dis-

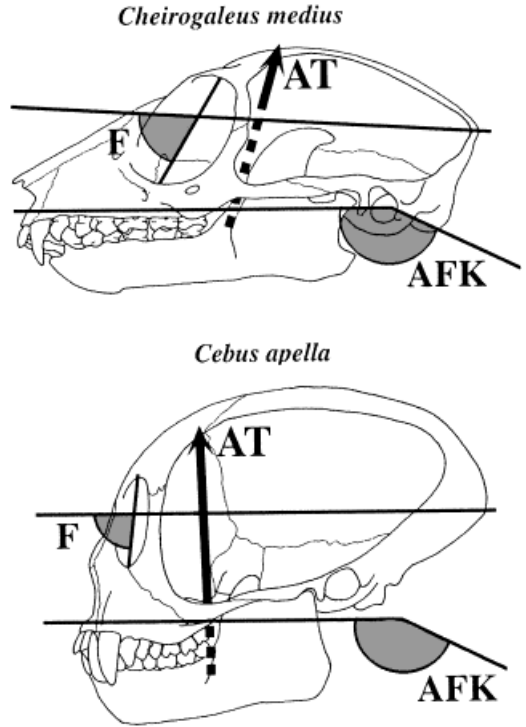


Fig. 7. Diagram illustrating the effect of increased orbital frontation (F) on the orientation of AT (line of action of anterior temporalis) relative to the palate. Both *Cheirogaleus medius* and *Cebus apella* have an AFK of 134°, but *Cebus*, like all anthropoids, has more frontated orbits (data from Ross, 1993). Increasing frontation drags the line of action of AT rostrally, making it more vertical.

placement of the superior orbital margin results in anterior displacement of the origin of the anterior temporal muscles, anthropoids also have anterior temporal fibers that are more vertically oriented relative to the palate than is the case in prosimians (Fig. 7). These anatomical data provide support for the catholic recruitment hypothesis (i.e., that stem anthropoids may have needed to maintain anterior temporal muscle mass because of its importance for a variety of chewing and biting activities). This hypothesis receives support from in vivo data gathered from jaw adductors during isometric biting in humans. Activity in the anterior temporalis is less affected by bite force direction than other parts of temporalis (Van Eijden, 1990; Van Eijden et al., 1990; Blanksma and Van Eijden, 1990).

The catholic recruitment hypothesis, however, did not receive strong support from the *in vivo* data presented here. The anterior temporal muscles were not consistently less variable in EMG amplitudes in comparison with other jaw muscles. How can these owl monkey *in vivo* data be reconciled with the anatomical data and with the human *in vivo* data? During isometric biting in humans, although the anterior temporalis shows less variation than other muscles, EMG amplitudes in the anterior temporalis and superficial masseter of humans do vary significantly with bite point and bite force orientation (Spencer, 1998; Van Eijden, 1990; Van Eijden et al., 1990; Blanksma and Van Eijden, 1990). The owl monkey data presented here were not gathered under conditions controlling for bite point or bite force orientation, and this may explain the discrepancy between these results and those on humans. Although the owl monkey anterior temporalis muscles do not exhibit less variable activity than other muscles across all biting and chewing behaviors, our data do not rule out the possibility that they are less variable at a given bite point and bite force orientation. Thus, because the anatomical data suggest that the anterior temporalis would be useful for a wide range of activities and because the anterior temporalis is active during a wide range of activities, we do not consider the catholic recruitment hypothesis fully falsified.

Muscle Function During Incision and Mastication

The data reported here do not corroborate the hypothesis that the anterior temporalis is more active than the masseter during incision, nor do they suggest that the anterior temporalis is more active during incision than during mastication of hard foods. On the contrary, activity of the masseter relative to that in the anterior temporalis is often higher during incision than mastication. This suggests that, as in macaques and humans, the masseter may be more important for producing bite force during incision than is the anterior temporalis, although the anterior temporalis still contributes significantly to incisive behaviors.

The data gathered in this study also provide no support for the notion that the anterior portion of the temporalis is more important for generating incisor bite forces than the posterior temporalis. No consistent differences in PTEMP/ATEMP ratios were observed between incision and mastication: sometimes the ratios were significantly higher during incision and sometimes lower. Thus, there is no reason to suggest that anterior temporalis muscle fibers taking origin from and lying against the post-orbital septum in *Aotus* are more important than the posterior temporalis fibers or the masseter during incision.

These results are similar to those obtained in similar experiments on humans and macaques (Hylander and Johnson, 1985). In 28 plots of averaged EMG values recorded in humans, five plots exhibited no consistent differences in relative anterior temporalis and masseter activity, 15 plots indicated masseter to be more active than the anterior temporalis during incision, and in eight plots the anterior temporalis was more active than the masseter during incision. Of 20 similar plots of averaged EMG values recorded from macaques, Hylander and Johnson found two plots indicating greater activity of the anterior temporalis during incision, while the remaining 18 plots exhibited greater activity in the superficial masseter during incision. Descriptive statistics of SMASS/ATEMP EMG ratios confirmed the patterns observed in both the human and macaque plots. Thus, whether the early anthropoids were catarrhine-like in possessing extensive muscle attachment on the postorbital septum (as suggested by Cachel, 1979) or platyrrhine-like in lacking extensive muscle attachment (as suggested by Ross, 1995b), the anterior temporal muscle fibers were not particularly important for powerful incision activities.

Postcanine Biting Hypothesis

The data gathered here do not provide strong support for the hypothesis that the anterior temporalis muscle is particularly important for biting along the postcanine toothrow. Although there is a general tendency for the anterior temporalis muscle to be more active than the superficial masseter

and posterior temporalis during biting along the postcanine tooththrow, and more active during biting along the postcanine tooththrow than mastication, these results are far from conclusive. However, when there were significant differences in anterior temporalis activity relative to other muscles, they tended to corroborate hypothesis 3, even without controlling for bite point position or bite force orientation.

CONCLUSIONS

Hypotheses that the postorbital septum evolved to protect the orbital contents from movements of the anterior temporal muscles (Cartmill, 1980; Ross, 1991,1993, 1994,1996) must explain why reduction in anterior temporal musculature was not a viable alternative to the evolution of the septum. It was hypothesized that the size of the anterior temporal musculature was maintained because this muscle is an especially important contributor to (1) bite forces during many different activities, (2) powerful incisor bite forces, and (3) powerful bite forces along the postcanine tooththrow. Owl monkeys are particularly appropriate for evaluating these hypothesis because they resemble the most likely primitive condition for anthropoids in not possessing extensive and tendinous origin for zygomaticomandibularis on the zygomatic portion of the postorbital septum. The muscle fibers arising from the postorbital septum are anterior temporalis fibers taking origin from the frontal portion of the septum.

The catholic recruitment hypothesis was not corroborated: Anterior temporalis was not found to be less variable in activity than other muscles across all behaviors. However, anterior temporalis was active during all behaviors, the anatomical data support this hypothesis, and variation in bite point position and bite force orientation may account for these results. The EMG data reported here do not corroborate the hypothesis that EMG magnitudes of anterior temporalis are greater than those of masseter during incision. In fact, EMG activity of anterior temporalis relative to the superficial masseter is lower during incision than during mastication and is not consistently more active than the posterior temporalis

during incision. Finally, this study provides weak support for the hypothesis that the anterior temporalis is particularly important during isometric biting along the postcanine tooththrow, suggesting that, although these results are not definitive, postcanine biting behaviors may have been linked to the evolution of the postorbital septum.

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