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Control of jaw movements in two species of macropodines (*Macropus eugenii* and *Macropus rufus*)☆

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Abstract

The masticatory motor patterns of three tammar wallabies and two red kangaroos were determined by analyzing the pattern of electromyographic (EMG) activity of the jaw adductors and correlating it with lower jaw movements, as recorded by digital video and videoradiography. Transverse jaw movements were limited by the width of the upper incisal arcade. Molars engaged in food breakdown during two distinct occlusal phases characterized by abrupt changes in the direction of working-side hemimandible movement. Separate orthal (Phase I) and transverse (Phase II) trajectories were observed. The working-side lower jaw initially was drawn laterally by the balancing-side medial pterygoid and then orthally by overlapping activity in the balancing- and working-side temporalis and the balancing-side superficial masseter and medial pterygoid. Transverse movement occurred principally via the working-side medial pterygoid and superficial masseter. This pattern contrasted to that of placental herbivores, which are known to break down food when they move the working-side lower jaw transversely along a relatively longer linear path without changing direction during the power stroke. The placental trajectory results from overlapping activity in the working- and balancing-side adductor muscles, suggesting that macropods and placental herbivores have modified the primitive masticatory motor pattern in different ways.

Keywords: Marsupials; Mastication; Neural control

1. Introduction

Marsupial herbivores and placental ungulates independently evolved dentitions and jaw movements suitable for the cropping and intraoral breakdown of plant material (Janis and Fortelius, 1988). Electromyographic signals (EMGs) of the adductor muscles controlling lower jaw movements during mastication have been recorded in several placental herbivores: goats (De Vree and Gans, 1975; Lieberman and Crompton, 2000; Crompton et al., in press), pigs (Herring and Scapino, 1973), rabbits (Weijs and Dantuma, 1981; Schwartz et al., 1989), primates (Hylander et al., 2000; Hylander et al., 2005), but in only one marsupial herbivore — the hairy-nosed wombat (Crompton et al., in press). Macropods have extremely mobile (Class I) symphyses (Scapino, 1981), which allow the hemimandibles to rotate around their longitudinal axes. During the last 160 years, several investigators have discussed the effect of a mobile symphysis on incisal and molar occlusion in macropods (Waterhouse, 1846; Murie and Bartlett, 1866; Anderson, 1927). The first detailed account of macropod jaw movements during mastication was that of Ride (1959). He confirmed that the lower incisors move closer to one another during occlusion and suggested that contractions of the medial pterygoid muscles were responsible both for inversion of the lower borders of the hemimandibles, and separation of the lower incisors during jaw opening. He further demonstrated that during jaw closure the lower jaw was swung towards the working side, and at the beginning of occlusion the buccal surfaces of matching upper and lower molars were in line with

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one another. The working-side lower molars were then drawn medially. Ride (1959) claimed that, because macropods are only slightly anisognathic, the balancing-side upper and lower molars contacted one another at the end of occlusion (lingual phase of occlusion: Mills, 1966); but he doubted that food was actually broken down between the balancing-side molars.

1.1. Phases of occlusion in macropod and placental herbivores

In a detailed study of the pattern of wear of the molars in wallabies and kangaroos, Sanson (1980, 1989) recognized two stages of jaw movement during molar occlusion: Phase I and II. These phases should not be confused with the terms used by De Vree and Gans (1975) to designate different parts of the masticatory cycle in goats.

In grazing macropods during Phase I the working-side lower jaw moves vertically and food is cut or sheared between the transversely oriented lophs of the upper and lophids of the lower molar crowns. The posterior surfaces of the lower protolophid and metalophid shear past the anterior surfaces of the matching upper protoloph and metaloph. The lophs and lophids are connected by mesiodistally-oriented links. As the molars continue to occlude, food is trapped between the lophs and lophids on one side and the lower and upper links on the other. During Phase II the working-side lower jaw is drawn medially and food is sheared or ground between the lophs and lophids on one side and the links on the other. Sanson (1980) claims that a very slight amount of anterior jaw movement that forces the lophids against the lophs occurs during Phase I in grazing macropods, but this is greater in browsing macropods. During occlusion the procumbent lower incisors remain within the upper incisor arcade. Consequently, the width of the arcade sets the limit of transverse jaw movements (Janis and Fortelius, 1988; Lentle et al., 1998; Lentle et al., 2003). Sanson (1989) claimed that only a slight rotation of the hemimandibles (eversion of the lower border) was necessary to bring the molar rows and lower incisors close enough to one another to prevent balancing-side occlusion. Lentle et al. (1998, 2003) documented jaw movements in the tammar wallaby (*Macropus eugenii*) with the aid of cineradiography and by observation of striation orientation on individual teeth. They showed that the lower incisors always operate within the upper incisal arcade during molar occlusion, and that incisal and molar occlusion occurs simultaneously. Lentle et al. (2003) confirmed that each hemimandible rotates around its longitudinal axis during occlusion, everting the lower border. They did not, however, divide occlusion into two phases.

The terms “Phase I” and “Phase II” have also been used to describe occlusion in living and fossil primates (Hiiemae and Kay, 1972; Kay and Hiiemae, 1974; Kay, 1978). During Phase I in higher primates the molars move into centric occlusion and the working-side lower jaw moves dorsally, medially and rostrally. During Phase II the lower jaw moves ventrally, medially and rostrally. Wall et al. (2006) have shown that in baboons (*Papio anubis*) very little adductor force is actually generated during Phase II and that almost all the crushing and grinding occurs during Phase I. They suggested that minimal force production during Phase II occurs not only in primates, but also in other placentals where Phase II wear facets have been identified: for example, the molars of the hyrax (*Procavia capensis*: Janis, 1979a,b) and the greater Indian rhinoceros (*Rhinoceros unicornis*: Fortelius, 1985). Some placental herbivores, including horses and bovids, lack biphasic occlusion. In these animals, the lower molars are drawn across the uppers molars without a change in the direction of jaw movement (De Vree and Gans, 1975; Fortelius, 1985; Crompton et al., 2006).

1.2. Musculoskeletal organization of the masticatory apparatus in macropods

The general organization of the adductor muscles in marsupial and placental grazers is, in broad terms, similar (Abbie, 1939; Ride, 1959; Turnbull, 1970; Kalvas, 1999). However, while placental herbivores have deep mandibular angles, most marsupials, including macropods, possess inflected angles. An inflected angle elevates the insertion areas of the medial pterygoid and superficial masseter relative to the skull base.

The macropod medial pterygoid can be divided into two parts: superficial and deep (Abbie, 1939). The superficial portion has a broad area of insertion on the dorsal surface of the inflected angle while the deep portion inserts on the medial edge of the inflected angle. The fibers of the medial pterygoid are oriented more horizontally in macropods than in placental herbivores and are well suited to draw the hemimandible medially and invert its ventral margin (Ride, 1959).

The superficial masseter originates on the medial surface of the anterior third of the zygomatic arch and inserts on the ventral surface of the inflected angle and extends to its medial edge. Acting alone, the superficial masseter can adduct, evert and draw the hemimandible medially. The deep masseter originates on the inner surface of the zygomatic arch and inserts on the masseteric ridge and external surface of the ascending process of the dentary. Its fibers are vertically orientated because (i) the zygomatic arch is not bowed away from the ascending ramus as it is in placental herbivores, and (ii) the masseteric ridge projects slightly laterally (Kalvas, 1999). The temporalis inserts on both faces of the ascending ramus of the mandible.

1.3. Muscle Triplet activity in placental and marsupial herbivores

Nearly all mammals chew unilaterally. Jaw movements are controlled by the differential contraction of working- and balancing-side muscle pairs. Weijs (1994) referred to three muscles as Triplet I: the working-side posterior temporalis, the balancing-side medial pterygoid and the superficial masseter). He observed that these three muscles worked together to move the working-side lower jaw laterally, their EMG activity peaking at the beginning of the power stroke. A complimentary set of muscles, referred to as Triplet II, included the working-side superficial masseter, the medial pterygoid and the balancing-side posterior temporalis. They moved the lower jaw vertically and medially during the remainder of the power stroke. Weijs (1994) argued, in addition, that the working- and balancing-side temporalis fire before the Triplet I and II muscles.

Vinyard et al. (2006b) modified Weijs' model and included the working-side anterior temporalis and deep masseter in Triplet I, and the balancing-side anterior temporalis and deep masseter in Triplet II. They accepted the balancing- and working-side medial pterygoids as belonging to Triplets I and II, respectively. In "primitive" mammals such as opossums (Crompton, 1995), tenrecs (Oron and Crompton, 1985), galagos (Hylander, 1984), tree shrews (Vinyard et al., 2006b) and lemurs (Vinyard et al., 2006a), jaw movements are essentially performed in the sagittal plane with a small component of medially directed movement during the power stroke. The time difference between the first of Triplet I and last of Triplet II muscles to reach peak activity is on the order of 15–20 ms (Vinyard et al., 2006b). Mammals such as ungulates, lagomorphs and anthropoids extend the duration of the power stroke by accentuating transverse jaw movements (Hiiemae, 1978; Weijs, 1994; Hiiemae, 2000; Langenbach and Eijden, 2001). In these mammals, the time between the first and last of the Triplet muscles to peak lasts longer: up to 200 ms in goats (Crompton et al., in press) and 120 ms in macaques (Hylander et al., 2000, 2005). In goats, the last Triplet II muscle to peak is the balancing-side posterior temporalis (De Vree and Gans, 1975); whereas in anthropoids (Hylander et al., 2000, 2005) and alpacas (Williams, in press) the balancing-side deep masseter peaks last.

The masticatory motor pattern in wombats, the only marsupial herbivore in which this has been determined, does not involve differential control of working- and balancing-side muscle pairs during the power stroke (Crompton et al., in press).

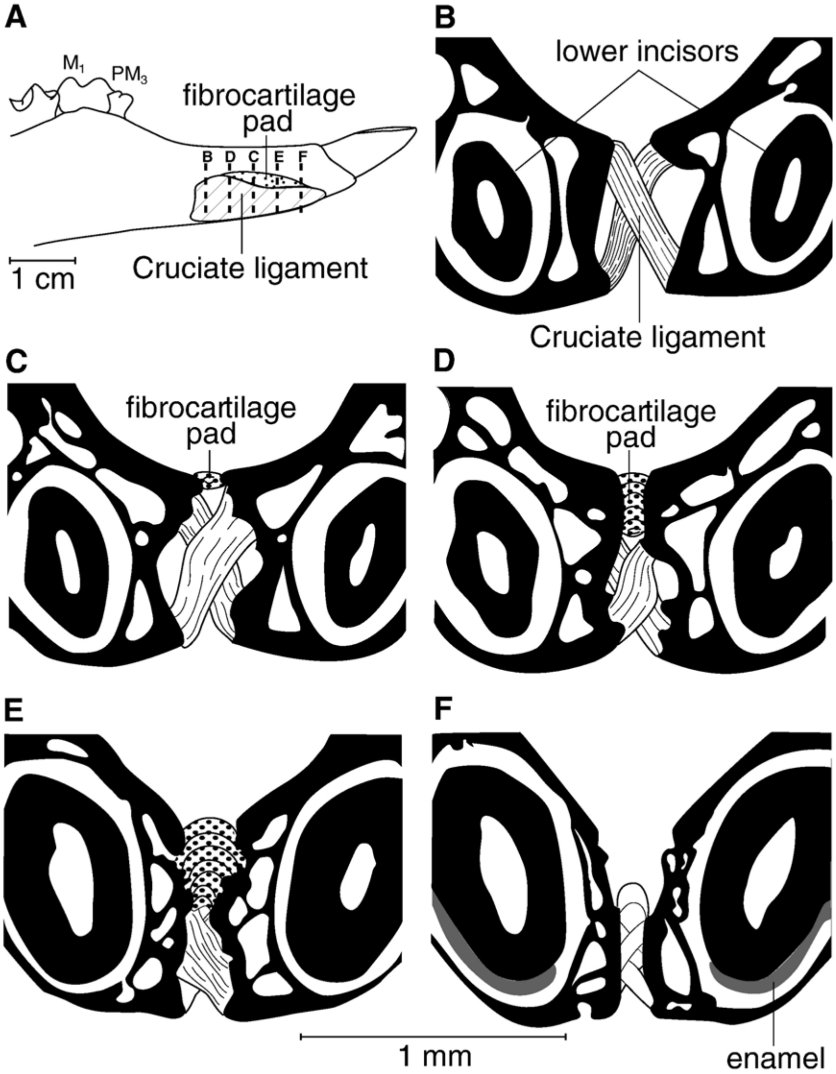

Fig. 1. Structure of the mandibular symphysis of the red kangaroo (*M. rufus*). (A) Sagittal section of the mandibular symphysis. The insertion area of the cruciate ligaments (cross hatched area) is below a narrow pad of fibrocartilage (dotted area). The vertical dotted lines labelled B–F indicate the position of five transverse sections shown in the remaining panels of the figure. In these panels, soft tissues are not included and only bone, incisor teeth, the fibrocartilage pad and the cruciate ligaments are shown. Note that the length of the cruciate ligaments decreases rostrad, and the orientation of the fibrocartilage pad is rostroventral — this suggests that the longitudinal axis of hemimandibular rotation is oblique. Arrangement of the cruciate ligaments permits independent hemimandibular rotation, and is suited for transfer of vertical adductor forces from the balancing to the working side. Abbreviations: M_1 — first molar, PM_3 — third premolar.

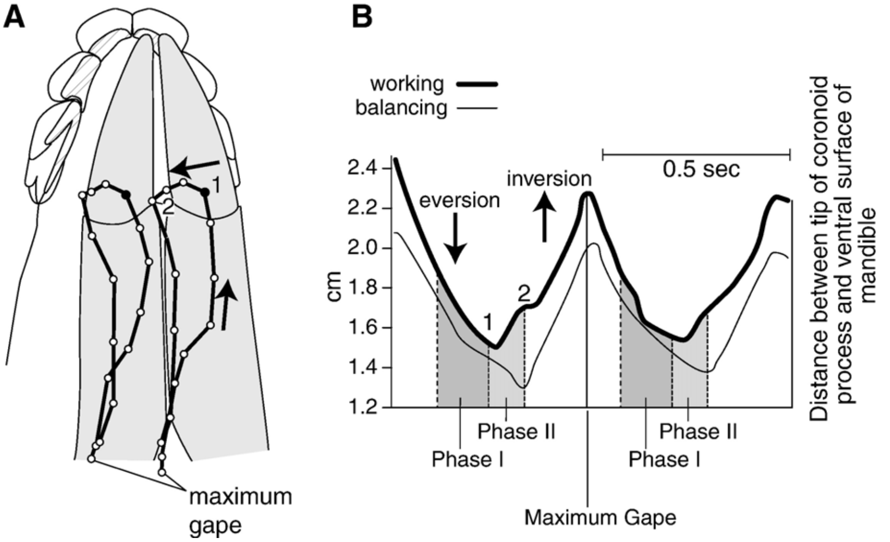

Fig. 2. Movement of the rostral region of the lower jaw during chewing in the tammar wallaby (*M. eugenii*), as viewed by videoradiography in an oblique (approximately 45°) dorsoventral projection. (A) Ventral view of the upper incisal arcade and position of the lower procumbent incisors and symphyseal region (shaded grey) at the end of Phase I. Solid lines show the orbits of movement of the balancing- and working-side radio opaque markers in the lower incisors. Small open circles on this line indicate marker positions for each video field (at 33 ms intervals) and the solid circle their position at the end of Phase I. During Phase II the working-side lower jaw moves (bold arrow) from position 1 to 2. Consequently, as the jaws open and close, the markers appear to move in a tear-shaped orbit between "maximum gape" to"1 → 2" to "maximum gape. (B) Graphic representation of the rotation of the hemimandibles during two chewing cycles. The balancing-side lower jaw (thin line) lags the working-side lower jaw (thick line) in maximum eversion by approximately 100 ms, but maximum inversion is almost synchronous on both sides. Filmed in dorsoventral projection, the lateral distance (*y*-axis) between the tip of the coronoid process and the ventral mandibular border provides a measure of rotation of each hemimandible. When the distance decreases, the ventral border of the hemimandible is everted, and *vice versa*.

In wombats only the working-side adductors are active during the power stroke and they alone are responsible for medially directed transverse jaw movement.

1.4. Force transfer across the symphysis

In general, bite force increases when forces generated by the balancing-side adductors transfer to the working side via the mandibular symphysis. The structure of the symphysis is often considered to reflect the magnitude and orientation of these forces (Ravosa et al., 2000; Hogue and Ravosa, 2001; Vinyard et al., 2006b). By comparing the amplitudes of adductor muscle EMGs during chewing sequences that include frequent side shifts, it is possible to determine the ratios of matching muscle pairs (*W*/*B* EMGs).

Strepsirrhines (galagos and lemurs) and tree shrews, which possess unfused/mobile mandibular symphyses, have relatively high (>1) *W*/*B* EMG and strain ratios. The *W*/*B* EMG ratios of the superficial masseter, anterior and posterior temporalis in galagos average 2.2, while the deep masseter ratios average 4.4 (Hylander et al., 2000). These ratios are confirmed by *W*/*B* mandibular corpus strains (*W*/*B* Strain), which can be as high as 7 in galagos (Hylander, 1984). Lemurs (Vinyard et al., 2006a) and tree shrews(Vinyard et al., 2006b) also have high *W*/*B* EMG ratios in the temporalis and masseter muscles. Vinyard et al. (2006b) argue that in order to maintain the structural integrity of an unfused/mobile symphysis during repeated chewing cycles, a limit is placed on the magnitude of balancing-side adductor force. Strengthening or fusion of the mandibular symphysis is required (Ravosa et al., 2000) before balancing-side forces can be increased to match those on the working side.

Crompton (1995) and Lieberman and Crompton (2000) showed that in two mammals with structurally different, unfused/mobile symphyses (opossums — Class I symphysis; goats — Class III symphysis), *W*/*B* EMG ratios were low during the chewing of hard food (in opossums, 1.1 for the combined adductor EMG activity; in goats, 1.3 for the superficial masseter, 1.8 for the deep masseter and 1.8 for the anterior temporalis). In an American opossum chewing bone, single element strain gauges placed on either side of the mandibular symphysis confirmed that balancing-side force is transferred through a Class I symphysis, without loss, to the working side (Crompton, 1995).

1.5. Aims

The purpose of this paper is to describe the activity patterns in the masticatory muscles of two closely related macropods: the tammar wallaby (*M. eugenii*) and the red kangaroo (*Macropus rufus*), and to compare them with those of placental herbivores.

We test three hypotheses:

1. In spite of the long independent evolution of marsupial herbivores on the Australian continent, we hypothesize that the masticatory motor pattern of macropods is similar to that of placental herbivores. This is based on the conclusion (Weijs, 1994) that the Triplet pattern occurs in extant "primitive" marsupials (opossums) and placentals (shews, tree shrews, galagos), and was probably present in their common ancestor. Furthermore, we expect that horizontal jaw movements in macropods will involve an overall increase in the duration of adductor muscle activity and in the

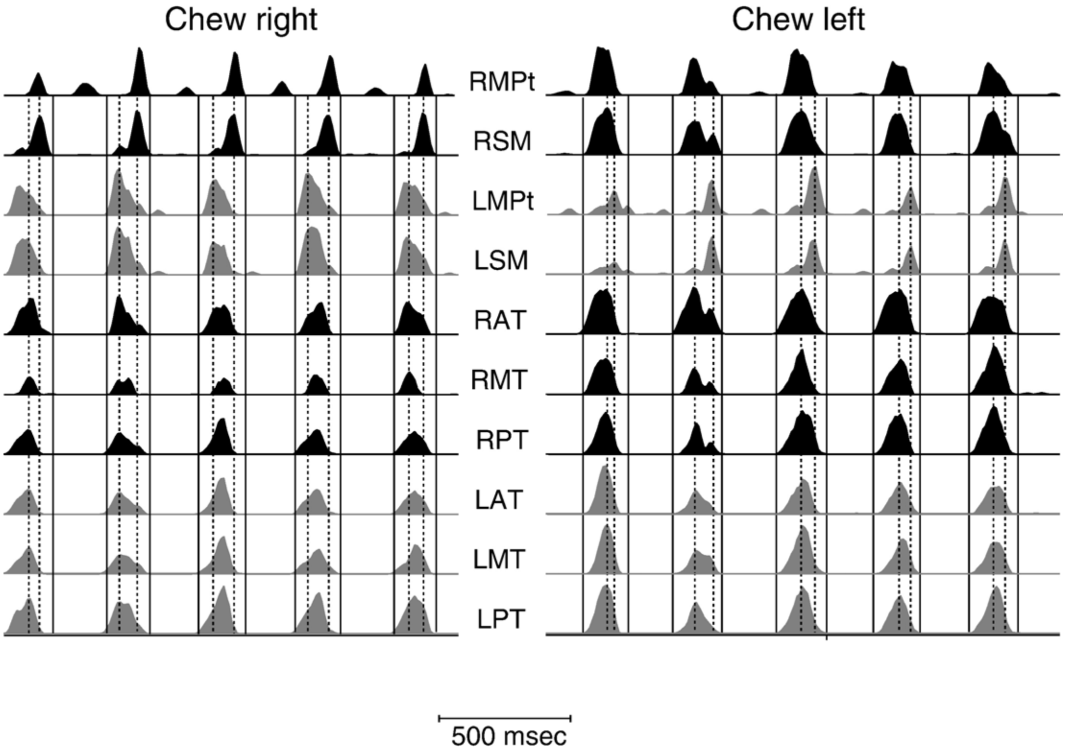

Fig. 3. EMGs of selected working- and balancing-side adductor muscles of a tammar wallaby (*M. eugenii*) during five chewing cycles (A) on the right, and (B) on the left side, during one continuous feeding sequence. Solid vertical lines span total adductor activity during each powerstroke cycle. Dotted vertical lines are drawn through peak activity in the balancing- and working-side superficial masseters. EMG activity of right-side muscles is shaded in black, and that of left-side muscles — in grey. The vertical axis for individual muscles is based upon the maximum amplitude recorded during the two feeding sequences (for explanation, see Section 2.5 in Materials and methods). Abbreviations: AT — anterior temporalis, B — balancing side, BAT — balancing-side anterior temporalis, BMPt — balancing-side medial pterygoid, BPT — balancing-side posterior temporalis, BSM — balancing-side superficial masseter, LAT — left anterior temporalis, LMPt — left medial pterygoid, LMT — left middle temporalis, LSM — left superficial masseter, MPT — medial pterygoid, MT — middle temporalis, PT — posterior temporalis, RAT — right anterior temporalis, RMPt — right medial pterygoid. RMT — right middle temporalis, RPT — right posterior temporalis, RSM — right superficial masseter, SM — superficial masseter, W — working side, WAT — working-side anterior temporalis, WMPt — working-side medial pterygoid, WPT — working-side posterior temporalis, WSM — working-side superficial masseter.

time lag between peak activity in Triplet I and Triplet II muscles, as suggested by Weijs (1994) and accepted by Hiiemae (2000) and Langenbach and van Eijden (2001).

2. We hypothesize that, as in placental herbivores that possess two phases of jaw movement during the power stroke, Phase I in macropods will also occur during peak activity in the adductor muscles and Phase II will occur when occlusal force is declining rapidly.
3. We predict large *W*/*B* EMG ratios of the jaw adductors in macropods because their slender unfused symphyses do not appear to be designed to transmit high, repetitive, vertically-oriented balancing-side forces to the working side.

2. Materials and methods

2.1. Animals

Two wild-caught juvenile red kangaroos were raised in the animal facilities of the University of Adelaide. Their exact age was unknown, but they were clearly juveniles that reached maturity during the course of the experiments. EMGs were recorded from Kangaroo #1 (female) in October 2001, again in November 2002 and finally in July 2004. Successful recordings from Kangaroo #2 (male) were only obtained in November 2002. EMGs were then recorded in three mature tammar wallabies, also housed in the outdoor animal facilities of the University of Adelaide, in August 2004. One mature tammar wallaby, raised at the Harvard University's Concord Field Station, was trained to feed in a Perspex box. Mastication was recorded videoradiographically in the X-ray suite of the Museum of Comparative Zoology.

2.2. Anatomy

Heads from carcasses of red kangaroos were obtained from Cleland Wildlife Park (South Australia). In order to confirm the position and orientation of the adductor muscles, one head was dissected and another one frozen and serially sectioned on a bandsaw into approximately 1 cm thick transverse slices. Because hemimandible rotation is reported to be involved during feeding, the symphyseal region of a red kangaroo was embedded in Osteobed (Polysciences Inc.), serially sectioned at 1 mm intervals on the IsometTM Low-Speed Saw (Buehler, Lake Bluff, IL, USA), glued onto microscope slides, and ground to approximately 100 μm for histological examination of the cruciate ligaments.

2.3. Surgery

Prior to surgery, all the animals were sedated with Zoletil (1 mg/kg, I.M.) then maintained at a surgical plane of anesthesia with isoflurane administered through a facemask. The ventral surface of the lower jaw and neck was shaved and sterilized. One incision was made in the midline below the posterior region of the lower jaw and another one further below the neck. A plastic tube (3 mm O.D.) was inserted below the skin between the two incisions. Six bipolar electrodes, made of 0.125 mm enameled copper wire and soldered to a 25-pin male connector, were fed forward through the tube. The tube was then withdrawn, leaving the electrodes below the skin. Using a 3-in, 20-gauge hypodermic needle, hooked tips of individual electrodes were inserted in the superficial masseter and the medial pterygoid on both sides through the anterior incision. (An attempt was made to insert one electrode in the superficial and one in the deep parts of the medial pterygoid, but because the animals were not sacrificed, the position of these electrodes could not be verified at the end of the experiment.) The incisions were closed with sutures and the 25-pin connector was held in place between the shoulder blades with bandages.

In Kangaroo #1 (2004) and all three tammar wallabies, six additional electrodes were inserted in the temporalis muscle. A medial incision was made over each animal's temporal region and back of the neck. Six electrodes were then led forwards through a plastic tube between the two incisions. Electrodes were inserted in the anterior, middle and posterior regions of the temporalis on both sides. The six ventral and six dorsal electrodes were connected to a 25-pin connector that was held in place with bandages.

Under isoflurane anesthesia, amalgam fillings were placed in the ventral surface of the procumbent power incisors of the tammar wallaby studied at the Museum of Comparative Zoology. In addition, the ventral surface of each hemimandible was exposed via an incision on the ventral surface of each hemimandible below M_3. A 1 × 1 cm piece of periosteum was removed and a small piece of silver wire (0.5 × 1 mm) adhered to the bone with superglue.

All surgical procedures had received prior approval by the Animal Ethics Committee at the University of Adelaide, and/or the Institutional Animal Care and Use Committee at Harvard University.

2.4. Recordings

Electrodes were connected to P511 J amplifiers (Grass Inc., Quincy, MA, USA) with a bandpass filter of 300 Hz to 3 KHz. EMG signals were amplified (×1000–×10, 000) to produce a signal of not more than 5 V. All data were recorded digitally on a

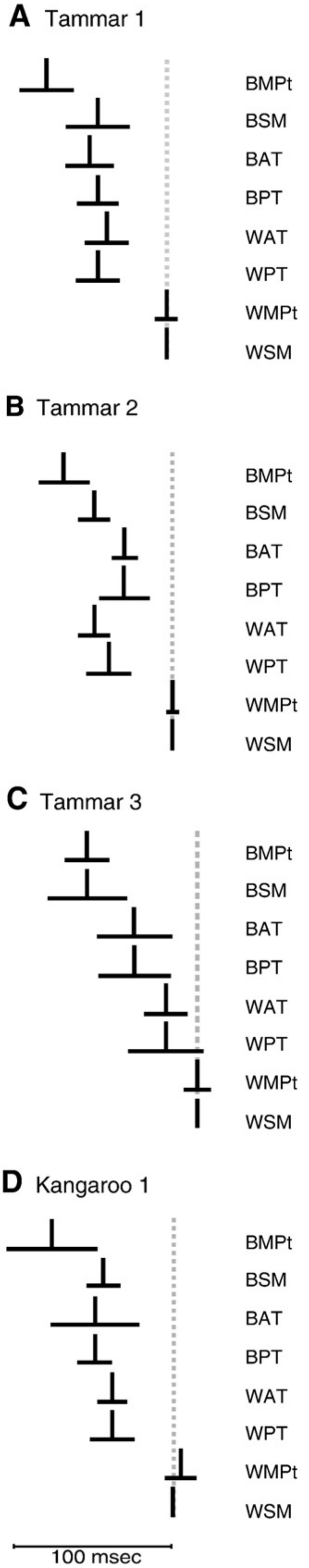

Fig. 4. Summary of timing differences in peak EMG activity of jaw adductors in three tammar wallabies (*M. eugenii*; A, B, C) and a red kangaroo (*M. rufus*; D). Vertical bars indicate the timing of median peak activity in working- and balancing-side adductor muscles relative to that of the working-side superficial masseter (at time 0, indicated by the dotted vertical line). Horizontal bars indicate ±one standard deviation. This figure is based upon the data given in Table 1. For abbreviations, see legend of Fig. 3.

Table 1
Timing differences in milliseconds between peak EMG activity in jaw muscles and peak of working-side superficial masseter in tammar wallabies and red kangaroos

Subject	*N*	Balancing medial pterygoid		Working medial pterygoid		Balancing superficial masseter		Balancing anterior temporalis		Working anterior temporalis		Balancing anterior temporalis		Working anterior temporalis	
		Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD
Tammar 1	20	−70	16	0	7	−40	18	−45	13	−35	12	−40	12	−40	13
Tammar 2	11	−70	18	0	14	−50	11	−30	8	−50	10	−30	16	−40	14
Tammar 3	11	−70	24	0	18	−70	25	−40	24	−20	14	−40	16	−20	23
Kangaroo 1 (04)	20	−100	27	5	9	−45	10	−50	26	−40	8	−50	10	−40	13
Kangaroo 1 (04)	20	−80	16	0	6	−45	17	−50	15	−40	15	−50	13	−40	15
Kangaroo 1 (01)	10	−60	39	0	6	−70	10								
Kangaroo 1 (01)	10	−70	10	0	7	−70	9								
Kangaroo 1 (02)	10	−85	18	0	14	−80	17								
Kangaroo 2 (02)	11	−70	12	0	1	−70	10								
Kangaroo 2 (02)	10	−70	6	0	6	−70	8								

TEAC™ RD-145 T DAT tape recorder (TEAC Corp., Tokyo, Japan).

Feeding behavior was recorded with a digital video recorder (DCR-TRV30, Sony Corp.). In order to synchronize the video and EMG data, a small light emitting diode (LED) was placed within the edge of the video field. Manually triggered short current pulses of varying duration to the LED were recorded synchronously with EMGs. Recorded data was played out on a 16-channel thermal array recorder (WR3600, GraphTec America, Santa Ana, CA, USA). Selected areas of at least 10 rhythmic chewing cycles were chosen for detailed analysis.

Videofluorographic images, via Tridoros 150G3 cineradiographic apparatus (Siemens, Germany), in dorsoventral, oblique and lateral views were captured with a Sony digital video recorder (as above).

2.5. EMG data analysis

Sections of EMG data that corresponded to video recordings of rhythmic molar chewing were subsampled at 6 kHz to reduce file size and transferred from the TEAC data recorder to a computer using TEAC's QuikVu II program. Custom-written software (copyright by David Hertweck) processed the raw EMG data in the following manner: it eliminated any offset, performed full-wave rectification, applied a constant time (10 ms), reset integration and rejected randomly-timed electrical activity (Thexton, 1996). The software finally displayed the processed EMG signals together with the video synchronization pulses.

Within each feeding sequence, amplification of the EMG signals was held constant and the maximum EMG activity of each muscle was scaled to 100 units. This equalized signal amplitude across electrodes despite inherent amplitude variations due to differences in the distance of electrodes from the nearest active muscle fibers.

The ratio of the adductor EMG activity on the working and balancing sides of the jaw was calculated as a ratio (*W*/*B*), using recordings of single feeding sequences that included side shifts or when side shifts were recorded in repetitive chewing sequences that entailed the same food and EMG amplification. The ratios were calculated in two different ways. The first was based upon the peak activity of the working- and balancing-side muscles without considering the time at which that peak activity occurred during the power stroke. The second was designed to determine *W*/*B* EMG ratios of all the muscles at two specific points in time: (a) when the balancing-side superficial masseter peaked, and (b) when the working-side superficial masseter peaked.

Identification of the chewing side could only occasionally be determined from the video recordings. However, synchronization of video images and EMG signals confirmed that a distinctive EMG pattern is associated with right and left chewing sides. This, in turn, allowed us to determine the chewing side for EMG sequences when the jaw was obscured in the video images.

Table 2
Tammar wallaby

	N	Working superficial masseter		Balancing superficial masseter		Working medial pterygoid		Balancing medial pterygoid		Working anterior temporalis		Balancing anterior temporalis		Working middle temporalis		Balancing middle temporalis		Working posterior temporalis		Balancing posterior temporalis	
		Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD
A. Median amplitude of peak activity in working- and balancing-side muscles																					
	10	50.0	13.0	74.0	11.1	48.0	18.0	79.0	15.9	46.0	12.6	74.0	11.8	31.0	11.3	77.0	11.5	43.0	12.5	64.0	13.0
B. Median amplitude of working- and balancing-side adductors at two points in time: Phase 1, at peak activity in the balancing-side superficial masseter; and Phase 2, at peak activity in the working-side superficial masseter.																					
Phase I	10	9.0	1.6	74.0	10.7	11.0	2.9	70.0	16.8	42.0	14.0	75.0	11.4	27.0	11.6	75.0	11.4	42.0	14.4	64.0	8.7
Phase II	10	50.0	12.8	15.0	4.7	49.0	14.0	8.0	2.9	11.0	1.8	12.0	2.7	10.0	1.4	15.0	3.8	10.0	1.2	9.0	3.6

Table 3
Tammar wallaby

		Superficial masseter		Medial pterygoid		Anterior temporalis		Middle temporalis		Posterior temporalis	
	N	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD
A. *W*/*B* ratios based on peak amplitudes											
	10	0.64	0.17	0.75	0.13	0.62	0.15	0.41	0.11	0.60	0.21
B. *W*/*B* ratios for individual muscles based upon when the balancing-side superficial masseter peaks (Phase I) and when the working-side superficial masseter peaks (Phase II)											
Phase I	10	0.12	0.03	0.14	0.07	0.61	0.07	0.39	0.11	0.58	0.26
Phase II	10	3.40	0.87	6.10	2.30	1.00	0.12	6.00	0.15	1.00	0.40

Integrated and rectified EMGs were displayed with Igor Pro v.4.0 (Wavemetrics Inc. Lake Oswego, OR, USA) which was also used to calculate: (a) the median and standard deviation of EMG amplitudes; (b) the *W*/*B* EMG ratios; (c) the cycle length and (d) the timing differences between median peak EMG activity in the adductor muscles on the one hand and peak activity in the working-side superficial masseter on the other (Hylander et al., 2000, 2005; Vinyard et al., 2006a,b).

2.6. X-ray image analysis

Videofluorographic images of a tammar wallaby feeding were acquired using Final Cut Pro software (Apple Inc.) and saved as MPEG files and JPEG image sequences. Movement of the radiopaque markers was analyzed by digitizing the position of the markers on individual video frames using NIH ImageJ.

3. Results

3.1. Structure of the mandibular symphysis

The macropod symphysis is deep posteriorly and tapers in the anterior direction. It consists of a slender dorsal fibrocartilage pad and a series of cruciate ligaments below (Fig. 1A). Relatively long (5 mm) and wide (1.5 mm) cruciate ligaments connect the dorsal margin of the symphysis of one hemimandible with the ventral border of the opposite hemimandible. At the posterior edge of the fibrocartilage pad (Fig. 1B), the cruciate ligaments are long. In the rostral direction (Fig. 1C–E), the fibrocartilage pad increases in depth and breadth, and the cruciate ligaments decrease in height. At the anterior edge of the symphysis (Fig. 1F), the cruciate ligaments are short and only a remnant of the cartilage pad remains. The cartilage pad appears to form an oblique longitudinal axis around which the two hemimandibles can rotate. As the dorsal insertion of the cruciate ligaments lies close to the axis of rotation the ligaments do not prevent independent rotation of the hemimandibles.

3.2. Jaw movements in the tammar wallaby

From the dorsoventral perspective, radiopaque markers in the hemimandible of each tammar wallaby traced tear-shaped orbits, and transverse movements of the lower incisors were restricted by the width of the upper incisal arcade (Fig. 2A). As the jaw closed, its working-side was drawn laterally until the lateral side of the working-side lower molars were positioned directly below the lateral side of the working-side upper molars. For approximately 132 ms, the lower jaw remained in a lateral position as the jaw moved in an orthal direction, allowing the transverse lophs of the upper molars to shear past the lophids on the lower molars. At the end of the orthal phase (Phase I of Sanson, 1980, 1989), the lophs and lophids met the links and the lateral surface of the lower procumbent incisor contacts the upper incisal arcade. Next, for approximately 100 milliseconds both hemimandibles moved transversely (Fig. 2A, ‘1’→‘2’), and the molar lophs and lophids dragged across the links (Phase II of Sanson, 1980, 1989). At the same time, the working-side lower incisor sheared past the upper incisors.

The working- and balancing-side hemimandibles rotated independently of the other (Fig. 2B). As the lower jaw closed, each hemimandible first moved dorsolaterally and then orthally (Phase I, Fig. 2B), everting its ventral border. As the lower jaw was drawn transversely (Phase II), the working-side hemimandible began to invert, while the balancing-side hemimandible continued to evert. The continuing eversion of the balancing-side hemimandible during Phase II decreased the width between the lateral edges of two lower incisors, and thus permitted increased transverse movement by the lower jaw within the upper incisal arcade. As the jaws opened to reach maximum gape, the ventral borders of both hemimandibles inverted.

3.3. Electromyography of jaw adductors in the tammar wallaby

In Tammar Wallaby #1 (Figs. 3, 4A, Table 1), the first muscle to reach its peak activity was the balancing-side medial pterygoid. The next set of muscles (balancing-side superficial masseter, and working- and balancing-side anterior, middle and posterior temporalis) fired about 25 ms later, peaking within 10 ms of each other. The balancing-side medial pterygoid and superficial masseter were best suited to move the working-side lower jaw laterally, while the temporalis (on both sides) was best suited to move it vertically. Acting together, this group of muscles appeared to be responsible for Phase I of molar occlusion. The working-side superficial masseter and medial pterygoid were the last muscles to reach peak activity.

In the other two tammar wallabies, the EMG pattern was much the same — the balancing-side superficial masseter and medial pterygoid were the first, and the working-side superficial masseter and medial pterygoid the last muscles to reach peak activity. However, there was more variation in the activity pattern of the temporalis than in the Tammar Wallaby #1, with the balancing-side temporalis sometimes peaking after the working-side temporalis

(Fig. 4B) and sometimes before it (Fig. 4C). In some chewing sequences the peak in the balancing-side superficial masseter activity lagged behind that of the balancing-side medial pterygoid (Fig. 4A and B), and sometimes was synchronous with it (Fig. 4C).

In all the tammar wallabies, the last two muscles to peak during the power stroke were the working-side medial pterygoid and superficial masseter. The working-side superficial masseter peaked 20–35 ms after the last region of the temporalis to peak. Rising activity in the working-side medial pterygoid and superficial masseter overlapped declining activity in all the other adductor muscles. These two muscles were best suited to move the working-side hemimandible medially and appeared to be responsible for Phase II of occlusion. The EMG pattern reversed as the chewing side shifted from right to left (Fig. 3).

With the EMG gains held constant during side shifts in single chewing sequences, it was possible with confidence to directly compare peak activity of balancing- and working-side muscles (Table 2), and use these data to determine working- to balancing-side (*W*/*B*) EMG ratios (Table 3). When median amplitudes of peak activity of individual adductors were compared, regardless of when peak activity occurred during the power stroke (Table 2A, Fig. 5A), there was a tendency of slight dominance of the balancing-side muscles in some sequences. In others, the ratios for the superficial masseter and medial pterygoid approach 1. Hence, the *W*/*B* EMG ratios were approximately 0.6 for the superficial masseter, 0.75 for medial pterygoid, 0.6 for the anterior temporalis; and between 0.4 and 0.6 for the middle and posterior temporalis (Table 3A).

Given there was a significant time gap between the last of the temporalis regions to peak and the peak of the working-side superficial masseter, it may be more appropriate to calculate *W*/*B* EMG ratios from specific time points during the power stroke. This provides a more realistic account of when, during power stroke, force was transferred from the balancing to the working side. There was an alternating pattern of dominance between the working- and balancing-side superficial masseter and medial pterygoid muscles. When the balancing-side superficial masseter peaked (Phase I), the amplitude of its activity and that of the balancing-side medial pterygoid overshadowed the activity of the same muscles on the working side (Fig. 5B). When the working-side superficial masseter peaked (Phase II), its amplitude and that of the working-side medial pterygoid were far greater than those of the corresponding balancing-side muscles (Fig. 5C). Activity levels of the three regions of the working- and balancing-side temporalis during both phases were closer to one another than in the working- and balancing-side superficial masseter and medial pterygoid, but overall activity in both sides of the temporalis was greater during Phase I than II. The *W*/*B* EMG ratios for the two phases are given in Table 3B.

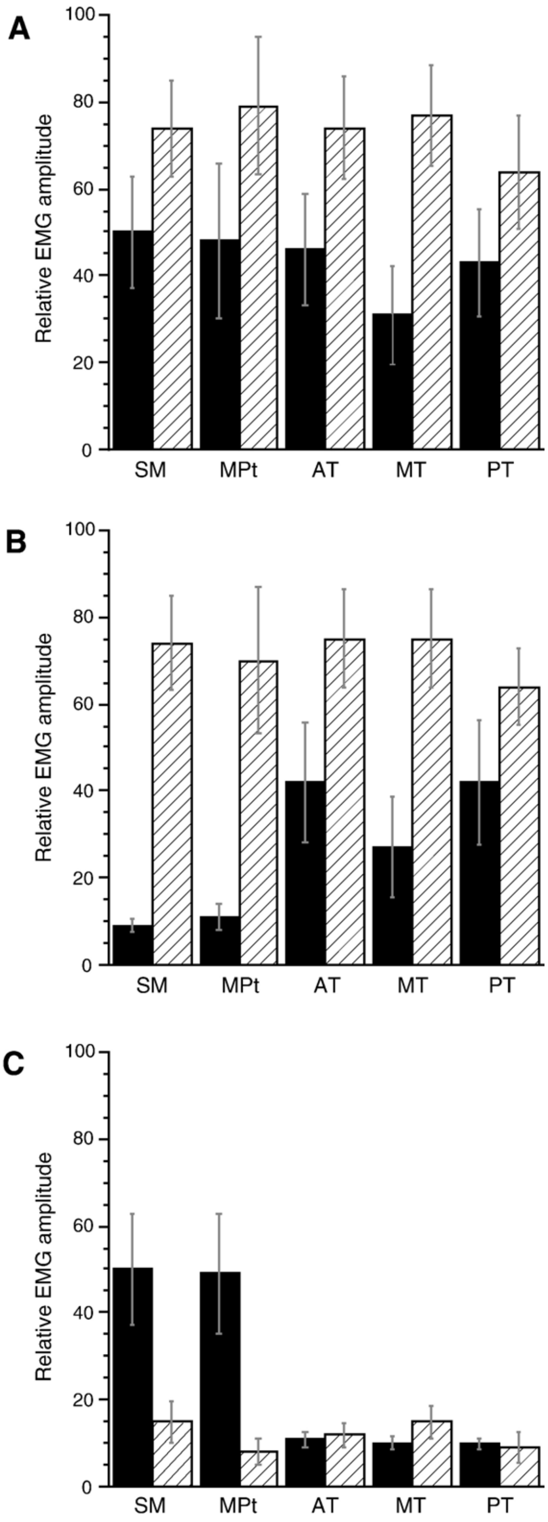

Fig. 5. Median levels of EMG activity in matching adductor muscle pairs of a tammar wallaby (*M. eugenii*). (A) Maximum activity of working- and balancing-side muscles during the entire power stroke. Activity of working- and balancing-side muscles measured at the time of peak EMG activity (B) in the balancing-side superficial masseter (Phase I) of molar occlusion, and (C) in the working-side superficial masseter (Phase II). Black bars indicate the working-side adductors, and light grey bars — the balancing-side muscles. Note the dramatic change in relative EMG activity of the superficial masseter and the medial pterygoid muscles during the two phases of occlusion: greater as balancing-side muscles during Phase I, and greater as working-side muscles during Phase II. In contrast, there is little difference between relative EMG activity of the temporalis as working- or balancing-side muscle. In general, however, the temporalis activity is significantly greater during Phase I than Phase II. This figure is based upon the data given in Table 2. For abbreviations, see legend of Fig. 3.

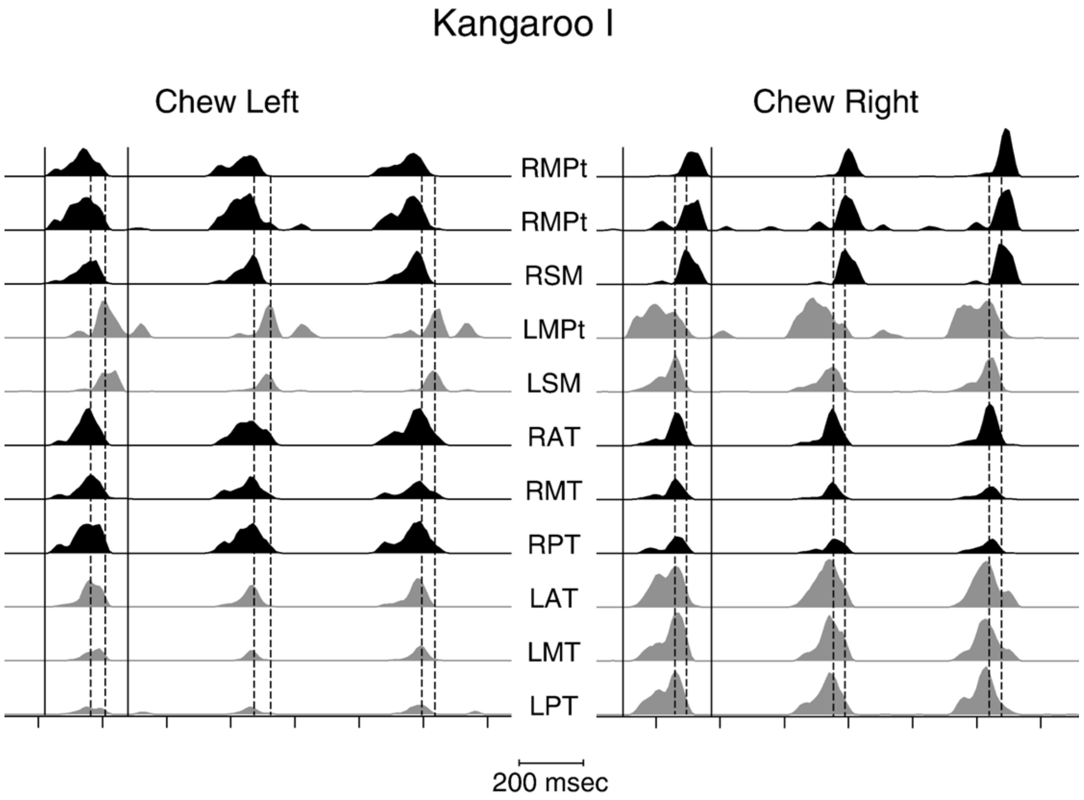

Fig. 6. EMGs of selected working- and balancing-side adductor muscle pairs of a red kangaroo (*M. rufus*) during three chewing cycles (A) on the left side, and (B) on the right side, during one continuous feeding sequence. Dotted vertical lines are drawn through peak activity in the balancing- and working-side superficial masseters. EMG activity of right-side muscles is shaded in black, and that of left-side muscles in grey. The vertical axis for individual muscles is based upon the maximum amplitude recorded during the two feeding sequences. For explanation, see Section 2.5 in Materials and methods. For abbreviations, see legend of Fig. 3.

In Tammar Wallabies #1, 2 and 3, the duration of chewing cycles (based upon the time between peaks of activity in the working-side superficial masseter) were 380 ± 25, 379 ± 23 and 425 ± 24 ms, respectively.

3.4. Electromyography of jaw adductors in the red kangaroo

The chewing EMG pattern of the red kangaroo was very similar to that of the tammar wallaby. The first muscle to peak (Figs. 4D and 6, Table 1) was the balancing-side medial pterygoid. The working-side superficial masseter and medial pterygoid were the last to peak. All the other muscles (anterior, middle, and posterior temporalis on both sides, and balancing-side superficial masseter) peaked within 20 ms of one another. A gap of 45 ± 15 ms separated the last of this group to peak from peak activity in the working-side superficial masseter and medial pterygoid. Cycle durations for two separate chewing sequences from Kangaroo #1 (obtained in experiments conducted three years apart, with electrodes sampling the activity of different motor units) and one Kangaroo #2 sequence were 520 ± 52, 520 ± 4 and 530 ± 26 ms, respectively.

When *W*/*B* EMG ratios were compared using median amplitude of peak activity of individual adductors, no matter when it occurred during the power stroke (Fig. 7A, Tables 4A and 5A), the ratio for the superficial masseter was 1.1 and for the medial pterygoid 0.97. The ratio for the anterior, middle and posterior temporalis was 0.85, 0.50 and 0.39 respectively. Consequently, levels of peak activity in working- and balancing-side superficial masseter and medial pterygoid were roughly equal at some point during the power stroke. In contrast, activity levels on the balancing side were always higher in all parts of the temporalis, although this was less marked in the anterior temporalis.

However, when the same *W*/*B* EMG ratios were calculated for the same muscles at two distinct points during the power stroke: Phase I, when the balancing-side superficial masseter peaked, and Phase II when the working-side superficial masseter peaked, a different pattern emerged. When the balancing-side superficial masseter peaked (Phase I), activity of the balancing-side adductors was much greater than that of the same muscles on the working side (Fig. 7B and Table 4B); and the *W*/*B* EMG ratio was low and always well below 1 (Table 5B). Activity in the balancing-side superficial masseter was 15 times greater than of the working-side superficial masseter, and 22, 1.2, 2.5 and 2.3 times higher in the balancing-side medial pterygoid and anterior, middle and posterior temporalis, respectively. During Phase II, when the working-side superficial masseter peaked (Table 4B and Fig. 7C), the *W*/*B* EMG ratios of the superficial masseter and medial pterygoid muscles were extremely high (Table 5B: 8.9 and 7.5, respectively). As the activity levels in the working-side medial pterygoid and superficial masseter rose towards their peak, activity in all the other muscles declined rapidly and was very low when the working-side medial pterygoid and the superficial masseter reached their peak (Fig. 6). This decline in activity was more rapid in the working-side than in the balancing-side temporalis. Consequently *W*/*B* ratios for the three regions of the temporalis during Phase II were low (Table 5B: 0.42, 0.32 and 0.78).

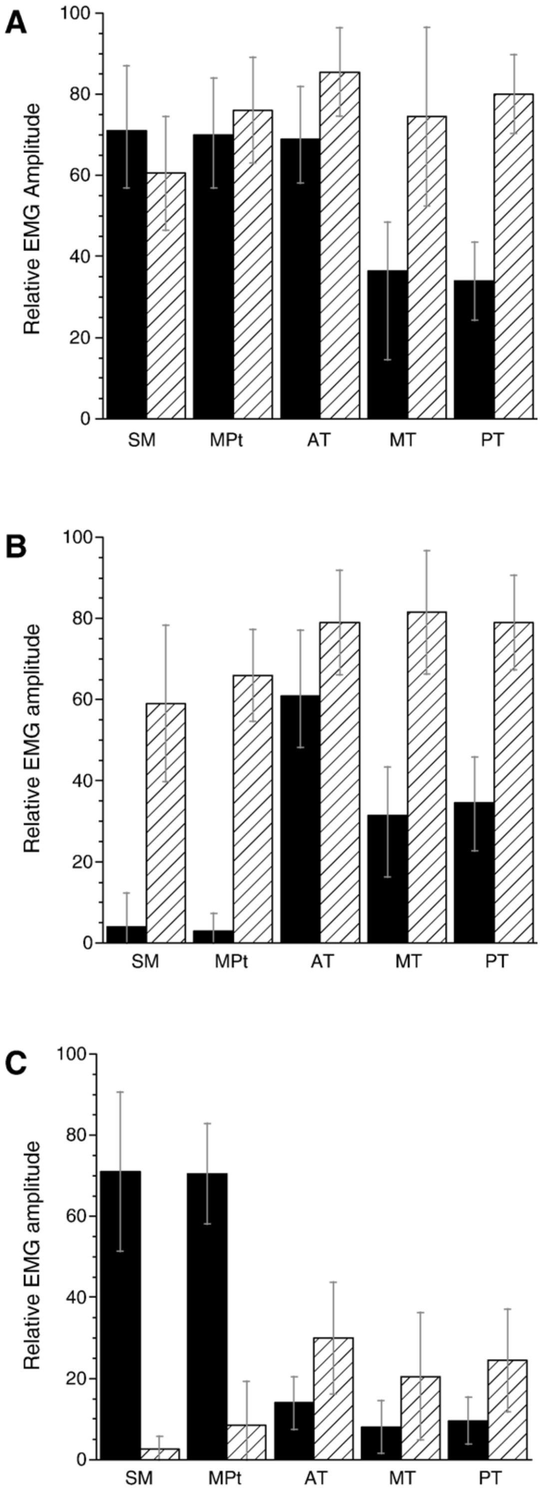

Fig. 7. Median levels of EMG activity in matching adductor muscle pairs in a red kangaroo (*M. rufus*). (A) Maximum activity of working- and balancing-side muscles during the entire power stroke. Activity of working- and balancing-side muscles measured at the time of peak EMG activity (B) in the balancing-side superficial masseter (Phase I) of molar occlusion, and (C) in the working-side superficial masseter (Phase II). Black bars indicate the working-side adductors, and light grey bars — the balancing-side muscles. As in the tammar wallaby EMG pattern, there is a dramatic change in relative EMG activity of the superficial masseter and the medial pterygoid muscles during the two phases of occlusion: greater as balancing-side muscles during Phase I, and greater as working-side muscles during Phase II. Again, there is little difference between relative EMG activity of the temporalis acting as working- or balancing-side muscle, but the temporalis activity is significantly greater during Phase I than Phase II. (A) is based upon the data given in Table 4A; (B) and (C) are based upon the data given in Table 4B. For abbreviations, see legend of Fig. 3.

4. Discussion

4.1. Masticatory motor pattern

Videoradiographic recordings of jaw movements of the tammar wallaby confirm that molar occlusion consists of two distinct phases: an initial orthal movement, followed by a medially directed movement in the transverse plane. As the jaw begins to close, the working-side hemimandible moves laterally and then vertically. Early activity in the balancing-side medial pterygoid and superficial masseter is associated with lateral jaw movement. Orthal movement correlates with overlapping activity in the balancing-side medial pterygoid, superficial masseter and temporalis, on both working and balancing sides; transverse movement is associated with activity in the working-side medial pterygoid and superficial masseter. Although the activity pattern of the deep masseter in macropods was not documented, it probably does not play a role in the mandible's transverse movement given its fibers' vertical orientation. The pattern of EMG activity in the adductor muscles of the red kangaroo during rhythmic chewing resembles that of the tammar wallaby. Further, the two types of jaw movements that occur in the tammar wallaby during occlusion are the same jaw movements that Sanson (1980, 1989) concludes occur during molar occlusion in kangaroos. He refers to the orthal movement as Phase I, and the transverse movement as Phase II.

The masticatory motor patterns of wallabies and kangaroos differ from that of placental herbivores, such as goats (De Vree and Gans, 1975; Lieberman and Crompton, 2000; Crompton et al., in press), rabbits (Weijs and Dantuma, 1981; Weijs et al., 1989), hyraxes (Janis, 1979a; Janis, 1979b; Janis and Fortelius, 1988), pigs (Herring, 1992) and higher primates (Hylander et al., 2000; Hylander et al., 2005). In all these placentals, a set of adductor muscles (Triplet I: balancing-side medial pterygoid and superficial masseter; and working-side deep masseter and posterior temporalis) initially draw the working side of the lower jaw dorsolaterally and then vertically to engage upper and lower molars. Subsequently, a mirror image of these muscles (Triplet II) draws the working-side hemimandible transversely. In goats and other artiodactyls, the working-side lower jaw moves along a relatively smooth and linear path, without a

Table 4
Red kangaroo

		Working superficial masseter		Balancing superficial masseter		Working medial pterygoid		Balancing medial pterygoid		Working anterior temporalis		Balancing anterior temporalis		Working middle temporalis		Balancing middle temporalis		Working posterior temporalis		Balancing posterior temporalis	
	N	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD
A. Median amplitude of peak activity in working- and balancing side-muscles																					
	20	71.0	16.4	60.5	14.0	70.6	14.0	76.5	13.0	69.0	13.0	85.5	10.8	36.5	12.3	74.5	22.1	34.0	9.5	80.0	9.7
B. Median amplitude of working- and balancing-side adductors at two points in time: Phase I, at peak activity in the balancing-side superficial masseter; and Phase II, at peak activity in the working-side superficial masseter																					
Phase I	20	4.0	8.4	59.0	19.3	3.0	4.3	66.0	11.3	61.0	16.0	79.0	12.8	31.5	11.9	81.5	15.2	34.5	11.4	79.0	11.7
Phase II	20	71.0	19.6	2.5	3.2	70.5	12.3	8.5	10.8	14.0	6.5	30.0	13.8	8.0	6.5	20.5	15.7	9.6	5.8	24.5	12.7

change in direction, during occlusion (Fortelius, 1985). This is in marked contrast to macropods where a clear change of direction occurs in jaw movement during occlusion: orthal followed by transverse.

Molar occlusion in some placental herbivores such as hyraxes (Janis, 1979a) and higher primates (Hiiemae and Kay, 1972; Wall et al., 2006) has also been divided into Phases I and II, but these phases do not correspond to the phases of molar occlusion in macropods. During Phase I in these placentals the jaw moves on a linear, mediodorsal path; during Phase II the jaw is drawn medioventrally while occlusal or near occlusal contact is maintained (Fortelius, 1985). It is unlikely that any significant breakdown of food occurs during Phase II in placentals (Wall et al., 2006) and no distinctive EMG pattern of activity is associated with this stage (Janis, 1979a; Wall et al., 2006). In macropods, on the other hand, the change in the direction of jaw movement during occlusion is clearly reflected in the EMG pattern, and foods are comminuted during both phases (Sanson, 1980, 1989).

To summarize, macropods and placentals herbivores appear to have modified a “primitive” masticatory motor pattern (Vinyard et al., 2006b)in slightly different ways: in placental herbivores, by increasing the time gap between peak activity in Triplet I and II muscles (Weijs, 1994); and in macropods, by adding the balancing-side temporalis to Triplet I and restricting Triplet II muscles to the working-side superficial masseter and medial pterygoid. The masticatory motor pattern of wombats (Crompton et al., in press) is quite different from that of both macropods and placental herbivores. Wombat jaw movements are transverse and linear throughout molar occlusion, but only the working-side adductors are recruited (Crompton et al., in press).

4.2. Molar and incisor occlusion

M. eugenii and *M. rufus* are selective grazers and crop small amounts of vegetation between the large lower procumbent incisors and the upper incisor arcade. The unique molar pattern of occlusion in these macropods may, in part, be related to the structure of the incisal region. Macropod incisors and molars occlude simultaneously; because the lower incisors remain within the narrow upper incisal arcade during occlusion (Janis and Fortelius, 1988; Lentle et al., 1998; Lentle et al., 2003) transverse jaw movement is limited to the width of the arcade. As suggested by Janis and Fortelius (1985), this may explain why macropods emphasize orthal jaw movements to break down food: the restriction on transverse jaw movements leads to the recruitment of both sides of the temporalis for orthal movement during Phase I. The limit on transverse movement is mitigated, to some extent, by rotation of the hemimandibles during jaw closure, since eversion of the lower borders of the hemimandibles draws the lower incisors and the lower molar rows closer to one another (Sanson, 1989).

4.3. W/B EMG ratios and mobile symphysis

When *W*/*B* EMG ratios in macropods were based upon peak activity in muscle pairs during chewing cycles, the ratios in the superficial masseter and medial pterygoid were close to or less

Table 5
Red kangaroo

		Superficial masseter		Medial pterygoid		Anterior temporalis		Middle temporalis		Posterior temporalis	
	N	Median	SD	Median	SD	Median	SD	Median	SD	Median	SD
A. *W*/*B* ratios based on peak amplitudes											
	20	1.10	0.50	0.97	0.29	0.85	0.16	0.50	0.14	0.39	0.13
B. *W*/*B* ratios for individual muscles based upon when the balancing-side superficial masseter peaks (Phase I) and when the working-side superficial masseter peaks (Phase II)											
Phase I	20	0.07	0.03	0.03	0.01	0.78	0.20	0.33	0.21	0.55	0.09
Phase II	20	8.95	1.29	7.50	1.36	0.42	0.09	0.32	0.15	0.78	0.28

than 1, and in the temporalis less than 1. This ratio indicates substantial recruitment of balancing-side muscles. However, because there was a time gap of 40–80 ms between Phase I and II muscle activity in tammar wallabies and kangaroos, *W*/*B* EMG ratios were calculated separately for each phase.

During Phase I, EMG activity was higher on the balancing- than working-side. This difference was especially true of the superficial masseter and medial pterygoid where *W*/*B* EMG ratios were extremely low and those of the temporalis were higher, but always below 1 (Tables 3B, 5B). This suggests that vertically-oriented forces generated by the balancing-side muscles during Phase I must be transferred to the working side via the cruciate ligaments of the mobile mandibular symphysis.

Phase II activity in the working-side superficial masseter and medial pterygoid far exceeded that of the balancing side whereas the *W*/*B* EMG ratio for the temporalis was well below 1. This suggests that transverse jaw movement during Phase II is effected primarily by the working-side superficial masseter.

Vinyard et al. (2006b) suggested that increased balancing-side jaw muscle force, together with a large number of daily chewing cycles, may result in fatigue-related damage to areas of the mandible likely to experience significant internal stresses during mastication. This presumably included the unfused mandibular symphysis. They concluded, "… we must consider the maintenance of structural integrity as an additional factor affecting the magnitude of balancing-side muscle-force recruitment during chewing." Dessem (1985) showed that when the adductor muscles were maximally stimulated in anesthetized domestic dogs, domestic cats and a raccoon during unilateral biting, 82% to 100% of vertical bite force transferred across an unfused symphysis from the balancing to the working side. Dessem (1989) and Dessem and Druzinsky (1992) showed, on the other hand, that when carnivores voluntarily bit with their carnassials, *W*/*B* EMG ratios were high, indicating reduced recruitment of balancing-side muscles. However, this probably had more to do with preventing mechanically disadvantageous jaw-joint forces than the inability of the mandibular symphysis to transmit high balancing-side forces.

Vinyard et al. (2006b) pointed out that Dessem's (1985) results, based upon maximally stimulated muscles, did not represent voluntary chewing or carnassial biting, nor did it rule out the possibility that maximal stimulation of the adductor muscles may injure the symphysis. However in opossums fed on hard food the *W*/*B* EMG and strain ratios were close to 1, indicating near equal EMG activity in both working- and balancing-side muscles (Crompton, 1995; Lieberman and Crompton, 2000). When opossums were fed only hard food (chicken bones with some flesh) for a period of twelve weeks, the vertical depth of the mandibular symphysis was increased to a greater extent than in animals of similar sizes and ages fed on soft food for the same length of time (Lieberman and Crompton, 1998). We concluded that this was in response to the larger vertical forces being transferred from the balancing to the working side via an unfused mandibular symphysis.

The extremely low *W*/*B* EMG ratios in kangaroos and wallabies during Phase I of molar occlusion indicate that despite their mobile unfused symphyses, they activate adductor muscles on the balancing side to an equal or greater extent than on the working side. There is no obvious reason why the recruitment of balancing-side forces should be so different in tree shrews and primates on the one hand and opossums and macropods on the other. Clearly, more data are needed on the recruitment of balancing-side muscle forces in a greater variety of animals to address the conflicting published results.

5. Conclusions

5.1. Hypothesis 1

Jaw movements in macropods are not controlled by the same Triplet masticatory motor pattern typical of placental herbivores. In placentals, the working-side lower jaw is drawn medially during the power stroke by a combination of working-side superficial masseter and medial pterygoid, and balancing-side posterior temporalis and deep masseter (so-called Triplet II muscles). In macropods the power stroke is divided into an orthal and transverse phase only the working-side superficial masseter and medial pterygoid draw the working-side lower jaw medially. In both placental herbivores and macropods the duration of the power stroke is increased.

5.2. Hypothesis 2

The neuromuscular control of the two phases of occlusion (Phase I and II) is fundamentally different in placental herbivores and macropods. In placentals effective breakdown of food occurs during Phase I when the working-side lower jaw is drawn medially; little or no breakdown occurs during Phase II as the jaws begin to open. In macropods food is broken down during both an orthal Phase I and a medially directed Phase II. During Phase I of placentals, medial movement of the lower jaw is controlled by a force couple generated by working- and balancing-side adductors (Triplet II). During Phase I of macropods, orthal movement of the lower jaw is controlled by synchronous activity of the temporalis on both sides, together with balancing-side masseter. It appears that a "primitive" Triplet motor pattern that was common to early insectivorous placentals and marsupials was modified in different ways by their herbivorous descendants. This reflects the long isolation of the Australian continent during the late Cretaceous and early to mid-Tertiary times.

5.3. Hypothesis 3

The slender mobile symphysis of macropods does not appear to limit the recruitment of balancing-side adductor muscles whose activity levels can equal or even exceed those on the working side. Except for the superficial masseter and medial pterygoid during Phase II, *W*/*B* EMG ratios are considerably less than 1, which implies considerable force transfer across the unfused symphysis especially during Phase I. We suggest that, in mammalian herbivores with a long occlusal phase, it is more informative to calculate *W*/*B* EMG ratios based not at peak activity of each muscle sometime during the power stroke, but on amplitude of working- and balancing-side muscles at two specific times during the power stroke.

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