Modulation of intra-oral processing in mammals and lepidosaurs

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Synopsis The mammalian masticatory apparatus is distinguished from the intra-oral processing systems of other amniotes by a number of morphological and functional features, including transverse movements of the teeth during the power stroke, precise occlusion, suspension of the teeth in the socket by a periodontal ligament, diphyodonty (reduction to two generations of teeth), a hard palate, and the presence of a single bone (the dentary) in the lower jaw which articulates with the skull at the temporomandibular jaw joint. The evolution of these features is commonly argued to have improved the efficiency of food processing in the oral cavity. The present aricle highlights the existence in mammals of the fusimotor system and afferent fibers from the periodontal ligament through which the CNS modulates the responses by the muscle spindles. Published data suggest that the fusimotor system and the periodontal afferents are important components in feed-forward (or anticipatory) control of chewing behavior. We hypothesize that this feed-forward control is used to maintain relatively constant cycle lengths in mammals in the face of intra-sequence and inter-sequence variation in material properties of the food, and that this enables them to maintain a higher average chewing frequency than that of lizards. These predictions were evaluated using data on mean cycle length and its variance from the literature and from our own files. On average, mammals have less variable cycle lengths than do lizards and shorter cycle lengths than do lizards of similar size. We hypothesize that by decreasing variance in cycle length, presumably close to the natural frequency of their feeding systems, mammals minimize energy expenditure during chewing, allowing them to chew for longer, thereby maintaining the high rates of food intake required for their high metabolic rates.

Introduction

Modulation is active *variation* in motor programs, kinematics or kinetics in response to changing external or internal conditions (Deban et al. 2001). The ability to modulate goal-oriented behavior in response to variation in environmental factors is an important aspect of vertebrate behavior. Intra-oral processing systems are fertile grounds for the study of modulation because the very nature of this processing produces variation in external and internal properties of food items to which there must be continuous adaptation. A wide range of vertebrates engages in intra-oral processing, including fish (Bemis and Lauder 1986), turtles, some birds, many lizards, and most mammals (Reilly et al. 2001), and it is likely that intra-oral processing is modulated to some degree in all these lineages.

The elevated metabolic demands of endothermy (Bennett and Ruben 1979), however, require mammals to ingest relatively more food than do other vertebrates, suggesting that mammalian mastication might be modulated more intensively or, at least, differently than the intra-oral processing of other vertebrates, thereby achieving faster, more efficient intra-oral processing with less wear on the teeth of the animal.

Modulatory abilities that reduce food processing time would be beneficial because intra-oral processing time is an important determinant of the rate of food intake in herbivorous mammals (Shipley et al. 1994). Although this may well be true for any vertebrate engaging in intra-oral processing, their higher food demands suggest that mammal intra-oral processing systems might work more quickly and/or

for longer periods of time than those of other vertebrates. Thus, mammalian masticatory systems are expected to be designed not only for increased temporal efficiency, but also for increased stamina. This increased stamina could be achieved through increased aerobic capacity in the feeding muscles (Bennett and Ruben 1979) and/or, as argued here, through adoption of rhythmic, cyclical chewing at or about the natural frequency of the feeding apparatus. Finally, because mammalian mastication involves application of (often) high bite forces between the hard but brittle enamel surfaces of the teeth for which only one replacement set is available, tight control of masticatory kinetics and kinematics would have the advantage of ameliorating deleterious effects of wear.

There is abundant evidence that bite force and jaw kinematics in mammals vary with material properties of the food both within and between chewing sequences (Thexton et al. 1980; Lavigne et al. 1987; Morimoto et al. 1989; Thexton and Crompton 1989; Hiiemae et al. 1996; Hidaka et al. 1997; Peyron et al. 1997; Thexton and Hiiemae 1997; Lund et al. 1998; Hiiemae and Palmer 1999; Buschang et al. 2000; Nakajima et al. 2001; Anderson et al. 2002; Peyron et al. 2002). Although modulation of chewing behavior is less well studied in nonmammalian vertebrates, jaw kinematics and the amplitude and duration of EMG bursts have been shown to vary in response to variation in food ''hardness'' (Herrel et al. 1999; Herrel et al. 2001) and the amount of work varies with different prey types (Andrews and Bertram 1997). Together these data suggest that the ability to vary motor output in response to variation in food properties may be common among vertebrates and that this variation is attributable to active responses of the organism and hence may be termed modulation.

Modulation can also be reflected in a decrease, or *relative lack of variation* in some behavioral parameter despite variation in external conditions. A good example of such modulation is the timing of movements of the jaw and tongue in frogs that use inertial elongation for tongue projection (Nishikawa 1999). Transfer of kinetic energy from the jaws to the tongue requires precise coordination of movements and variation in kinematics has significant impacts on the efficiency of the behavior. Hence, low levels of kinematic variation can be just as important an indicator of modulation as are high levels.

We argue that low levels of kinematic variation might also be expected in musculoskeletal systems that are used cyclically for long periods. The theoretical advantage of minimizing variance in length of the cycle is that it makes the chewing system function more efficiently. When an oscillating system functions close to its natural frequency, energy expenditure is minimized (Hatsopoulos 1996; Hatsopoulos and Warren 1996). In the feeding system this effect is most important at the level of the muscles that move the jaws, enabling them to contract for more cycles before becoming depleted of energy. Readers may appreciate this effect by chewing pieces of gum more quickly than their normal chewing rate, rapidly producing fatigue in the chewing muscles. Assuming that the variance in cycle length is minimized around the chewing system's natural frequency, minimal variance ensures that the system can operate for longer without fatigue, thereby facilitating more intra-oral processing per food item, and longer feeding bouts overall.

A second potential advantage of minimizing variance in cycle length around the system's natural frequency is a lower average cycle length, and more cycles per unit time (i.e., higher average chewing frequency). This advantage will accrue if it is easier—and therefore, more likely—for cycle length to be increased above the natural frequency than to be decreased below it. One important factor tending to bias variance in cycle length towards longer cycles is the extra energy required to generate muscle force as contraction time decreases. This effect would not eliminate cycles faster than the optimum, but it would mean that there would be a limit to the number of faster cycles that could be performed.

Thus, we hypothesize that (1) mammals chew more rhythmically (i.e., with less variance in cycle length) than do lizards in the face of variation in properties of the food within and between chewing sequences. We also hypothesize (2) that mammals have higher average chewing rates than do similarly sized lizards. Lepidosaurs (squamates and *Sphenodon*) are an ideal group to compare with mammals because (1) many lepidosaurian species are known to engage in significant intra-oral food processing (i.e., chewing) (Herrel et al. 1996; Herrel and Vree 1999; Herrel et al. 1999; Schwenk 2000a, 2000b; Reilly et al. 2001), (2) data on mean cycle length and its variance are available for more squamates than for any other amniote clade outside of mammals, and (3) we have direct access to much of these data as part of ongoing comparison of feeding behavior in lizards and mammals (by A.H. and C.F.R.).

Table 1 Descriptive statistics of the mean cycle lengths and CVs of *complete sequences* of noningestion chewing cycles for *individual* lepidosaurs and mammals

Individuals and species	Mean cycle length (ms)	Number of cycles	SD	CV
Lepidosaurs				
Agama stellio	681.79	67	292.26	42.87
Agama stellio	821.20	50	532.75	64.88
Agama stellio	764.44	27	228.66	29.91
Agama stellio	1589.29	28	955.86	60.14
Corucia zebrata	362.93	82	124.25	34.24
Corucia zebrata	301.89	53	194.31	64.37
Pogona vitticeps	251.14	233	106.29	42.32
Pogona vitticeps	278.69	287	125.06	44.87
Pogona vitticeps	222.88	475	71.71	32.18
Pogona vitticeps	232.47	482	450.12	193.62
Pogona vitticeps	239.56	101	96.04	40.09
Tiliqua rugosa	441.54	52	92.70	21.00
Tiliqua rugosa	443.87	31	119.49	26.92
Tiliqua scincoides	543.86	535	175.46	32.26
Tiliqua scincoides	593.41	528	204.78	34.51
Tiliqua scincoides	699.37	120	217.29	31.07
Tiliqua scincoides	500.35	80	129.45	25.87
Tupinambis merianae	480.10	429	187.90	39.14
Tupinambis merianae	503.36	324	222.71	44.25
Uromastix acanthinurus	754.89	47	341.03	45.18
Uromastix acanthinurus	623.64	22	148.85	23.87
Varanus niloticus	707.22	118	282.78	39.98
Varanus niloticus	661.81	340	1506.90	227.69
Varanus niloticus	475.56	9	205.48	43.21
Mammals				
Aotus trivirgatus	320.82	401	70.01	21.82
Aotus trivirgatus	500.32	205	117.03	23.39
Aotus trivirgatus	442.28	183	106.54	24.09
Macaca mulatta	827.32	193	101.65	12.29
Macaca mulatta	684.63	43	109.55	16.00
Otolemur crassicaudatus	472.82	11	46.81	9.90
Varecia variegata	348.25	57	69.81	20.05
Varecia variegata	329.62	108	67.61	20.51

Materials and methods

Sample

To evaluate the hypothesis that mammals employ rhythmic, repetitive chewing in spite of variation in food material properties and in cycle "type" (i.e., capture, transport, processing), we have collated data on mean cycle lengths and variance in cycle length in lepidosaurs and mammals both from the literature and from our own data files (Table 1).

Cycle length is known to be affected by food material properties both within and between chewing sequences in mammals (De Gueldre and De Vree 1984, 1988; De Dötsch 1986). Variation in cycle length also arises in association with variation in the processes (e.g., processing and transport) being performed within a cycle. Lizards, turtles, and birds have been said to process and transport food in different cycles (Smith 1982, 1984; Gans et al. 1985; Gans and De Vree 1986; Bels and Goosse 1989; Goose and Bels 1992; So et al. 1992; Zweers et al. 1994; Herrel et al. 1997; Herrel and Vree 1999), but not all studies have been able to distinguish between chewing and transport cycles on the basis of kinematics (Kraklau 1991; Delheusy and Bels 1992; Urbani and Bels 1995), and some have reported differences between chewing and transport cycles only in EMG amplitudes (Herrel et al. 1996, 1997). In mammals, mastication and transport can occur in the same cycle, albeit to different degrees depending on cycle "type", although transport and mastication cycles are kinematically distinct in cats (Thexton et al. 1980; Thexton and Mcgarrick 1988, 1989). Chewing cycles in mammals are divided into puncture crushing cycles and tooth–tooth contact cycles, on the basis of kinematic differences and on inferences about the presence or absence of tooth–tooth contact. Similarly, swallow cycles, which are usually slightly longer than nonswallow cycles, are either intercalated between subsequences of mastication cycles (Hylander et al. 1987; Thexton and Hiiemae 1997), or occur at the end of a chewing sequence. In this study, we make no attempt to discriminate between these different cycle types, other than to identify swallow cycles in lepidosaurs.

Published data on cycle length and our own data both derive from two sources: video recordings of animals feeding and analog recordings of electromyographic (EMG) or bone-strain data. Cycle-length data were extracted from video data by counting the number of frames between the beginning and end of a cycle and multiplying by the time represented by each frame. Different workers use different points in the cycle to define the beginning and the end. Some define a cycle from maximum gape to maximum gape, others from minimum gape to minimum gape (Schwartz et al. 1989). Although this might affect the number of cycles included in a particular sequence by excluding the first or last cycle in some cases, it will not have a significant impact on estimates of either mean cycle length or of variation in cycle length. Data on length of cycle were also extracted from analog data files by calculating the time from peak bone strain or peak EMG activity in a major

jaw adductor during the closing phase in one cycle to peak bone strain or EMG in the closing phase of the next cycle.

Variables

As expected, the magnitudes of the mean standard deviations for each species are correlated with the mean length of cycle. To control for this effect, standard deviations were re-expressed as percentages of the mean cycle length, i.e., as coefficients of variation (CVs) for use in comparisons between individuals and species.

Comparisons

Testing the predictions of our hypothesis regarding variance in cycle length requires comparisons of CVs in mammals with those in lepidosaurs. These comparisons were performed on six separate samples.

Comparisons of CVs of individuals (CV_i) across complete sequences

The most powerful tests of the hypothesis are comparisons between CVs of cycle length calculated at the level of individual animals. Estimates of variation within individuals capture variation due to differences within feeding sequences associated with cycle type (i.e., mammals: puncture/crushing, tooth–tooth contact, stage I transport, processing, stage II transport, swallowing; lepidosaurs: transport [including analogs of stage I and II in mammals and inertial transport], processing, pharyngeal packing, swallowing, and tongue-flicking); as well as variation within and between feeding sequences due to material properties of food. To fully capture variation in cycle length associated with cycle types, complete chewing sequences are needed. Hence, our first group of analyses compared the CV_is of lepidosaurs and mammals using only data from complete sequences.

Comparison 1A compared CV_is of all noningestion (where ingestion includes capture or attempted capture) cycles in the chewing sequences. Comparison 1B sought to determine whether the mammals showed less variance in cycle length when only processing or chewing cycles were considered. To do this, the CV_is of lizards were calculated after excluding all swallow, inertial transport, and tongue-flick cycles. The remainder was assumed to be transport cycles and/or processing cycles. Although it has been argued that transport and processing cycles can be distinguished in some lepidosaurs on the basis of jaw kinematics and jaw muscle EMGs, this distinction cannot always be made. This, combined with the fact that intra-oral transport

is such an integral part of intra-oral processing in mammals, suggests that it may not be reasonable to attempt such a distinction for lizards. The question of whether or not to include swallow cycles is more difficult, but we opted to include mammalian swallow cycles but exclude lizard ones for two reasons. First, whether they intercalate multiple swallows into a feeding sequence (primates) or only have one swallow at the end of the sequence, mammals usually swallow in the slow open phase of a cycle in which processing also occurs. This makes it difficult in practice and suspect in theory to exclude swallows from most of the data sets considered here. Second, although mammalian swallow cycles are slightly longer than nonswallows, lepidosaur swallows are often much longer than other cycles in that sequence (Throckmorton 1980; Delheusy and Bels 1992; Herrel et al. 1996; Herrel and De Vree 1999; Herrel et al. 1999). By excluding the lepidosaur swallows and including mammalian ones, we make the most conservative test of the hypothesis that mammal cycle lengths are less variable than those of lizards.

Comparisons of CVs of individuals (CV_i) across complete sequences, plus incomplete sequences, or sequences not known to be complete

Data are not always available for complete sequences. Reasons for this include technological limitations (e.g., limits to buffer size in A/D converters) and effects of sampling. The latter arise because most research studies have focused on specific activities during a feeding sequence, often rhythmic mastication, and deliberately exclude cycles associated with, for example, swallows, stage I transports or side shifts. Although such data sets provide underestimates of overall variance in cycle length during a feeding sequence, they provide significant increases in the number of individuals and species that can be sampled. Our second group of analyses therefore compares CV_is of lepidosaurs and mammals calculated using cycle-length data from complete sequences, incomplete sequences, and sequences of unknown completeness. Comparisons 2A and 2B consisted of the same data subdivisions as those in 1A and 1B.

Comparisons of species mean CVs (CV_m)

Published data on cycle lengths and their variances often pool data from multiple individuals while separating it by food type and/or cycle type. This has the effect of pooling intra-individual variation due to cycle type and food properties with variation due to inter-individual factors such as size. While these data
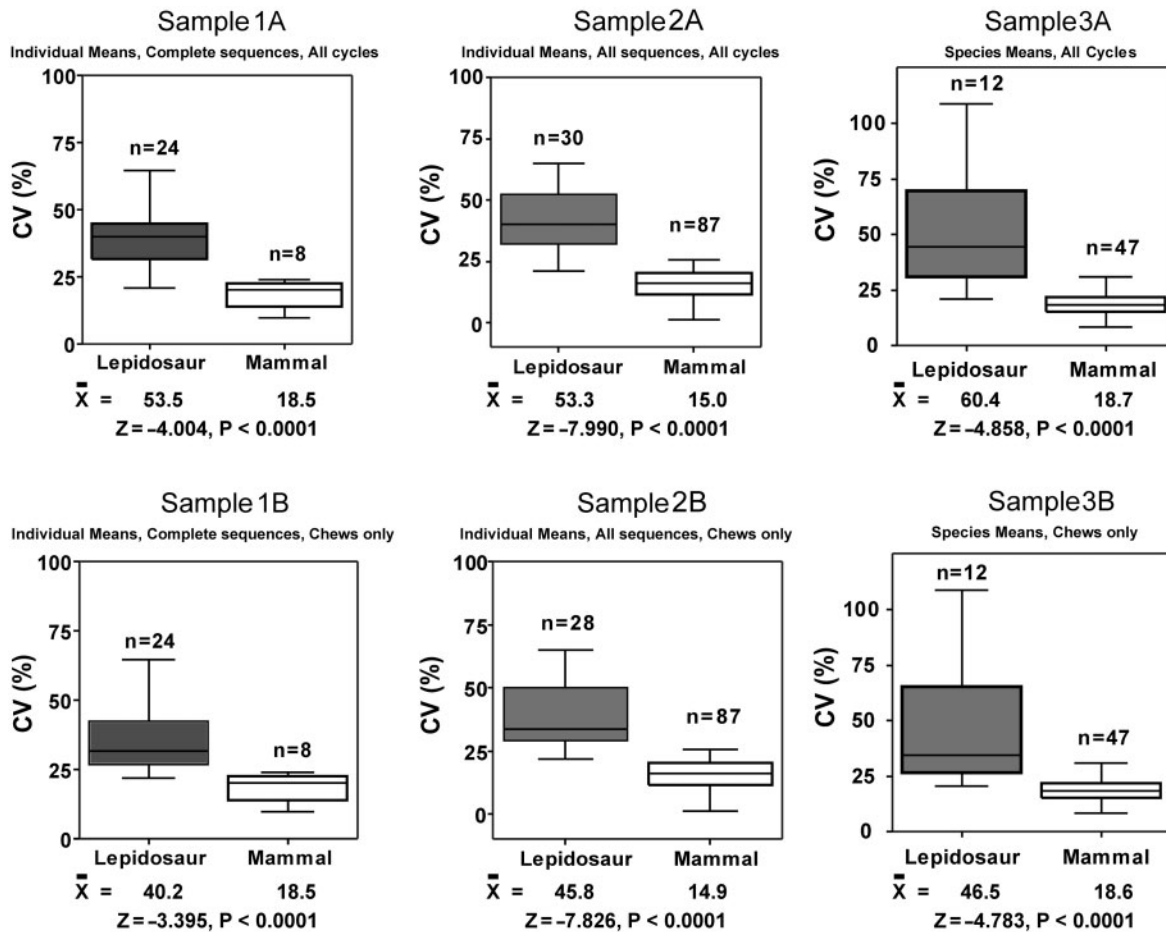
Fig. 1 Box plots and results of Mann–Whitney U-tests of all six samples. On average, mammals have less variable cycle lengths than do lepidosaurs.

are not ideal for the present study, they once again make it possible to include data from otherwise unsampled species, and to include data on variation in cycle length associated with additional food types. Almost all of the published data from which these CV_m calculations were made are from incomplete sequences.

To calculate CV_m from data in the literature, weighted averages were calculated of mean cycle lengths and of standard deviations across all food types and cycle types (except ingestions), where the weights were the number of cycles on which the means and standard deviations were based. CV_ms were then calculated from these weighted averages. Mean CVs (CV_m) were calculated by species from the data sets discussed in section "Comparisons of CVs of individuals across complete sequences, plus incomplete sequences or sequences not known to be complete," in combination with the data from the literature. Once again, Comparisons 3A and 3B were made using the same data subdivisions described under 1A and 1B.

Body mass and jaw length

When possible, data on jaw length and body mass were obtained from the same animals from which other data were collected. For the mammals in which these data were not available, measurements of jaw lengths were obtained from museum specimens and estimates of body mass were taken from the literature.

Statistical analyses

CVs were calculated for each of the six samples described and are presented in Table 1. Mean CVs calculated for mammals and lepidosaurs were tested for normality, skewness, kurtosis, and homoscedasticity before plotting and statistical comparison (Fig. 1). Samples violated assumptions of parametrics, so nonparametric Mann–Whitney U-tests were used to compare mean CVs. Means, Z-values for Mann–Whitney U-tests, and P-values are given in Fig. 1 below the box plots. Histograms of Cv_is and CV_ms are presented in Figs 2–4. To compare mean
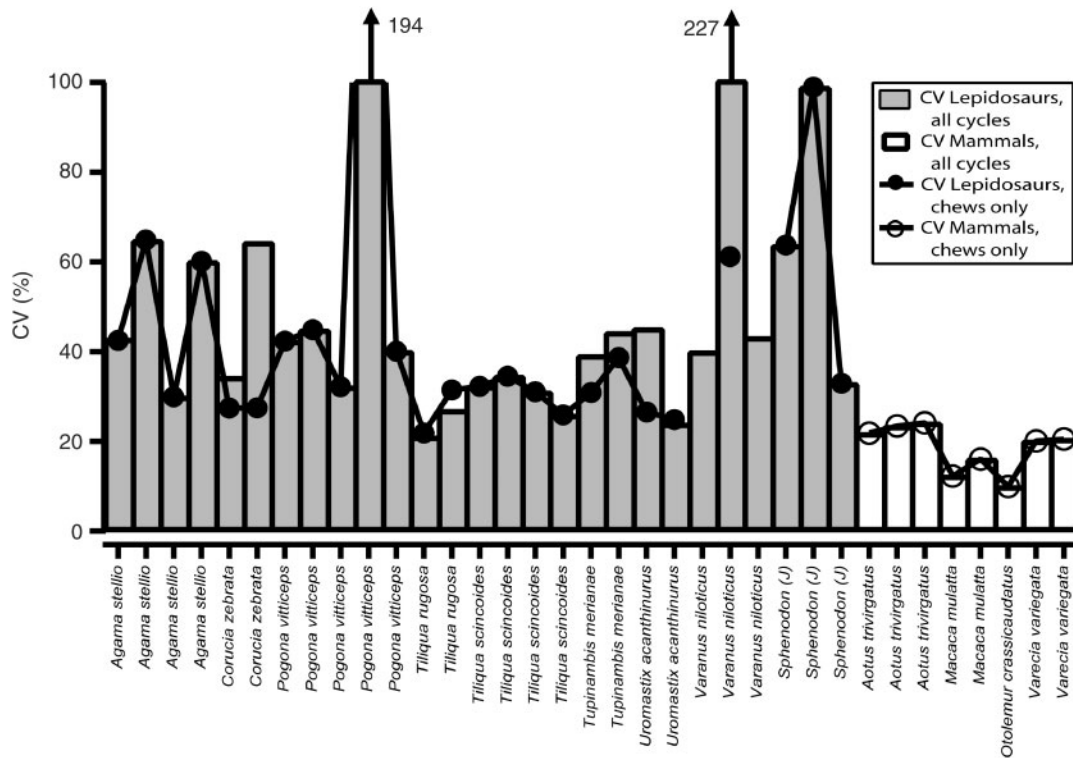
Fig. 2 Histogram of CV$_i$s (standard deviation expressed as a percentage of mean cycle length within each individual) for Samples 1A (bars) and 1B (lines and circles), i.e., mean CVs for individual lepidosaurs and mammals were calculated only from complete sequences. Sample 1A includes all cycles. Sample 1B only includes only chews.
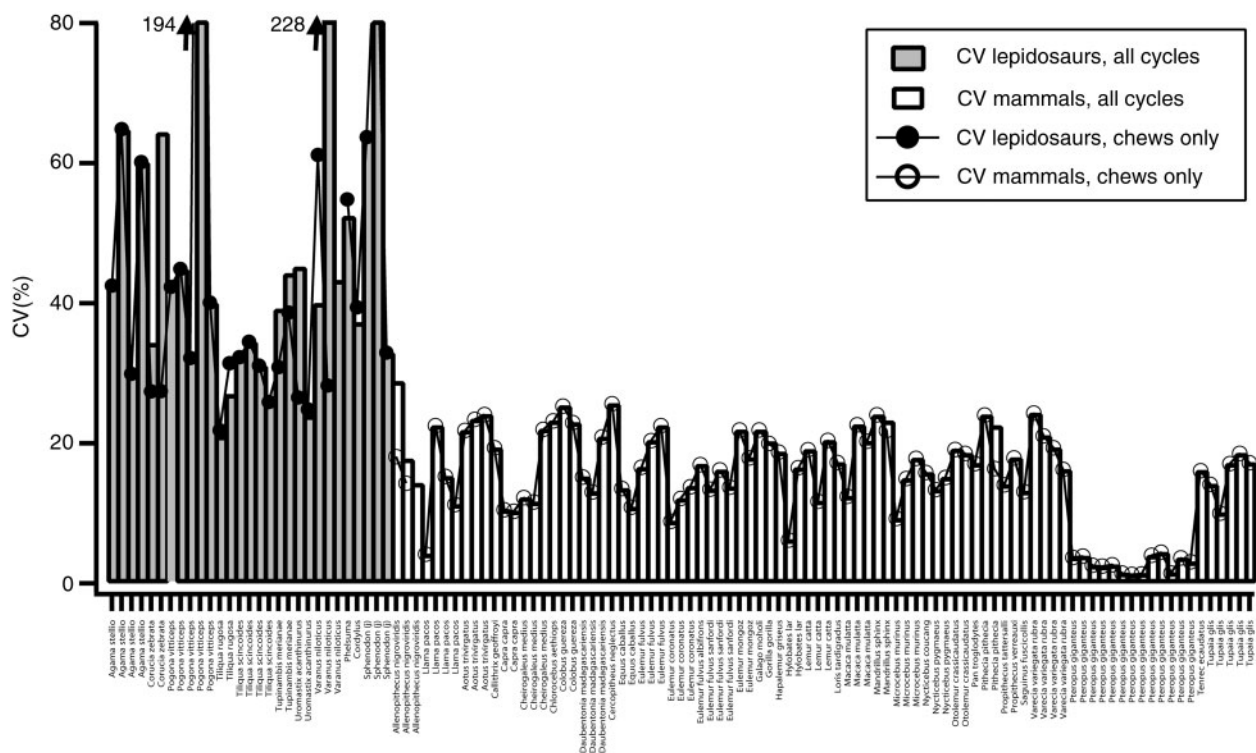

Fig. 3 Histogram of CV$_i$s (standard deviation expressed as a percentage of mean cycle length within each individual) for Samples 2A (bars) and 2B (lines and circles), i.e., mean CVs for individual lepidosaurs and mammals were calculated from all available sequences, complete and incomplete. Sample 2A includes all cycles. Sample 2B includes only chews.
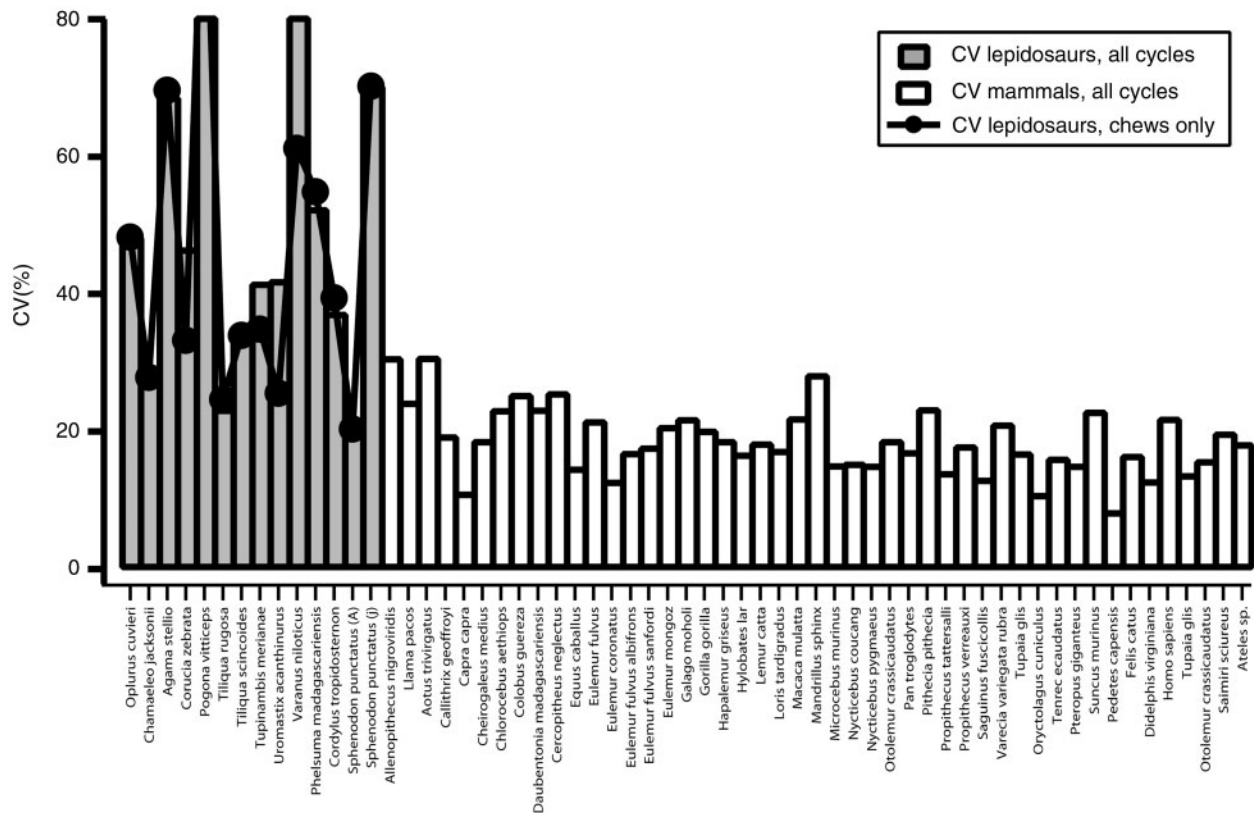
Fig. 4 Histogram of CV_ms (standard deviation expressed as a percentage of mean cycle length within each species) for Samples 3A (bars) and 3B (lines and circles), i.e., mean CVs for lepidosaur and mammal species were calculated from all available sequences, complete and incomplete. Sample 3A includes all cycles. Sample 3B only includes chews.

cycle lengths in lepidosaurs and mammals, mean cycle length was plotted against jaw length and body mass in the two groups (Fig. 5). Cycle length is known to be affected by body size in mammals (Druzinsky 1993; Shipley et al. 1994; Washington et al. 2005) and it is possible that such an effect is also seen in lepidosaurs.

Effects of sample size, mean cycle length and body size on standard deviations and CVs were examined using bivariate plots and correlation analyses.

Results

Comparisons of CVs of individuals (CV_i) across complete sequences

In both samples 1A and 1B, the CV_is for mammals are normally distributed but those of lepidosaurs are not; in both cases the CV_is for lepidosaurs are highly leptokurtotic, and skewed to the right. Log-transformation did not produce normal distributions for lepidosaurs, so the means were compared using nonparametric statistics. Mann–Whitney U-tests reveal that in both samples the means are significantly different, whether all cycles are considered, or just chews (Fig. 1). When all cycles are included,

lepidosaurs have a mean CV_i of 53.5% compared with only 18.5% for mammals. When only chews are included, the lepidosaurian mean CV_i decreases to 40.2%, compared to 18.5% for mammals. Examination of the histogram of CV_i for all individuals for which complete sequences are available confirms that individual lepidosaurs have more variable cycle lengths than individual mammals when complete sequences are compared (Fig. 2).

Comparisons of CVs of individuals (CV_i) across all sequences, complete, incomplete, or of unknown completeness

In both samples 2A and 2B, neither the CV_is for lepidosaurs nor those for mammals are normally distributed; in both samples the CV_is for lepidosaurs are highly leptokurtotic, and skewed to the right, whereas those for mammals are skewed to the left. Log-transformation did not produce normal distributions, so the means were compared using nonparametric statistics. Mann–Whitney U-tests reveal that in both samples the means are significantly different, whether all cycles are considered or just chews (Fig. 1). When all cycles are included, lepidosaurs have a mean CV_i of 53% compared with
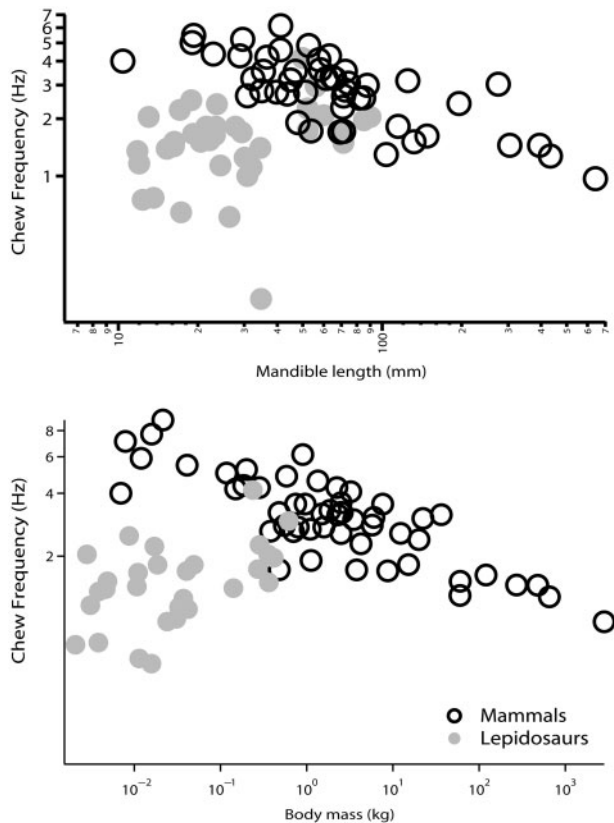
Fig. 5 Bivariate plots of mean chew frequency (1/cycle length) (Hz) against jaw length (mm) and body mass (kg) in lepidosaurs and mammals. Data from lepidosaurs are given in Table 3. Data from mammals are from Druzinksy (1993), Fortelius (1985), and Washington et al. (2005).

only 15% for mammals. When only chews are included, the lepidosaur mean CV_i decreases to 45.8%, compared to nearly 15% for mammals. The histogram of CV_i confirms that individual lepidosaurs have more variable cycle lengths than mammals when all available data are considered (Fig. 3).

Comparisons of species mean CVs (CV_m)

In neither sample 3A nor 3B are the CV_ms for lepidosaurs distributed normally; in sample 3A the CV_ms for lepidosaurs are leptokurtotic, and in both samples the CV_ms for lepidosaurs are skewed to the right. The CV_ms of mammals are normally distributed. The means were compared using Mann–Whitney U-tests (Fig. 1). In the case of both samples the means are significantly different, i.e., all cycles are considered or just chewing cycles. When all cycles are included, lepidosaurs have a mean CV_m of 60.4% compared with only 18.7% for mammals. When only chews are included, the lepidosaur mean CV_m decreases to 46.5%,

compared to 18.6% for mammals. On average, lepidosaur species exhibit more variable cycle lengths than do mammalian species (Fig. 4).

Mean chew frequency in lepidosaurs and mammals was plotted against body mass and jaw length in Fig. 5. Most lepidosaur species sampled clearly have lower chew frequencies (longer cycle lengths) than do mammals of equivalent jaw lengths or body masses. Because chew frequency scales with different slopes in the two groups, comparison of the chew frequencies in the two groups with ANCOVA is not possible. Instead chew frequencies of mammals and lepidosaurs were compared across the range of body sizes and jaw lengths encompassed by lepidosaurs only. Lepidosaurs have longer cycles than do mammals of equivalent body masses ($t = 5.73$, df $= 112$, $P < 0.0001$) or mandibular lengths ($t = 8.50$, df $= 82$, $P < 0.0001$).

Discussion

The data presented here demonstrate that, on average, lepidosaurs have intra-oral food processing cycles of more variable lengths than do mammals. The strongest support for this conclusion comes from comparisons of CVs within individuals (Figs 1–3), but is also supported by estimates calculated within species (Figs 1 and 4). We argue below that these differences in variance of cycle length between lepidosaurs and mammals are attributable to differences in modulatory abilities which can be linked to differences in the sensorimotor systems of the two groups. However, we first address some potential limitations in the data set that arose because the data were collated from the literature and from our files without controlling two factors that might have impacted the variance of cycle length: type and size of food item. Properties of the food have been shown to impact the length of the chew cycle in mammals, albeit with varying effects, so it needs to be determined whether the results from lepidosaurs are due to their being fed foods with a wider range of material properties than was the case for the mammals. The other factor that might affect variance of cycle length is size of food item. As most lizards ingest prey whole, relative prey size tends to be large in the wild, and this is usually replicated in the laboratory setting. The relatively large prey may then impose the need for an increase in time of contact between tongue and food to ensure that there is the adequate adhesion to successfully retract the tongue with adhering prey into the oral cavity. Thus, rather than being constrained by efficiency, lepidosaurs may be

constrained by tongue fitting and may thus need relatively longer cycles. Several lines of evidence suggest that differences in type and size of food item do not explain the differences in variance of cycle length documented here.

First, as is clear from Table 2, many of the mammals, especially the primates studied in the Ross laboratory, were fed a wider range of types of food item than were many of the lizards. Whether the greater number of different food items fed to the mammals was associated with greater variability in material properties of the food cannot be evaluated at present because material properties for the food items fed to the lepidosaurs, especially the live prey, are not available. It is clear, however, that many mammals had much less variable cycle lengths than did lizards that ate a smaller number of different types of food.

Second, although most of the data from lepidosaurs were taken from feeding sequences on animal prey (mealworms, crickets, grasshoppers, and mice) the sizes of which were not controlled, and the data from mammals derive primarily from chewing sequences involving plant items, the sizes of which were controlled, three sets of data suggest that consumption of animal versus plant food does not explain the differences in variance of cycle length (Fig. 6). In the first set of data, the impact of prey type on variance of cycle length was controlled by calculating CVs for individual mammals and lizards eating the one animal item that they ate in common: meal worm (Fig. 6A). When the CVs of the individuals were compared, mammals had significantly lower CVs than did lizards, even when *Agama stellio*, which displays a much higher CV than do other lepidosaurs, is excluded from the data set. Although it is possible for individual lizards to have lower CVs than those of some mammals, on average CVs of lizard's cycle lengths are larger than those of mammals eating the same food. The second test involved comparing CVs of cycle lengths in lizard and mammal individuals eating plant foods. This test simultaneously evaluates the effects of food item size on CV (plant food item size was usually controlled in the data sets of both lepidosaurs and mammals) and asks whether the higher CVs of cycle length in lepidosaurs are seen when the animals ate plants. Comparison of the CVs reveals mammals to have, on average, less variable cycle lengths than do lepidosaurs when both groups eat plant food (Fig. 6B). Some lizards also ate apple and when only complete sequences were compared, individual mammals had lower CVs than did individual lizards. (*Aotus*, $n = 116$ chews, $CV = 19.04$; *Varecia variegata*,

$n = 74$, $CV = 19.42$; *Corucia zebrata*, $n = 9$, $CV = 20.24$; *Corucia zebrata*, $n = 5$, $CV = 21.93$). Together, these data suggest that when eating both plant and animal food, mammals have lower variance of cycle length than do lizards. The third data set tests whether individual lizards that included both plants and animals in their diet exhibited more variable cycle lengths when eating animals than when eating plants. In the two *Tiliqua* and two *Uromastix* available for comparison, the CVs of sequences in which plants were eaten did not differ consistently from those in which animals were consumed; in each species, one individual exhibited more variable cycle lengths when eating plants and the other when eating animals (Fig. 6C).

Clearly, data from more carefully controlled experiments are needed to precisely define the effects of variation in type and size of food on variation in cycle length in lepidosaurs and mammals. Moreover, it is of interest that one or two of the individual lizards sampled do have CVs of cycle length lower than those of one or two of the mammals sampled. Nevertheless, we believe that the data presented in Figs 1–4 suggest that mammals have, on average, less variable cycle lengths than do lizards across a wide range of food material properties and cycle types.

The data presented here also suggest that mammals have shorter cycle lengths, and higher chewing rates, than do similarly sized lizards (Fig. 5). This is true whether or not the size of the feeding system or the size of the body are considered. These data corroborate the hypothesis that decreased variance of cycle length contributes to lower mean cycle lengths in mammals. Increased variance will be associated with increases in mean cycle length if it is more likely to increase variance by having longer cycles than shorter ones. Support for this assumption derives from the observation that the distribution of cycle lengths in lizards were usually skewed to the right rather than to the left. In comparison with lizards, mammals appear to decrease variance of cycles by eliminating the longer cycles, resulting in relatively lower average cycle lengths.

Mammals also exhibit a negative correlation between jaw length and chew frequency—longer jaws are associated with lower chew frequencies—but this relationship is not evident in lizards. One explanation for the pattern seen in mammals is that the natural chewing frequency decreases with increasing body size, thereby conserving the energy expended to move the system. Such optimization that minimizes energy expenditure is more likely in the feeding system of mammals than in lepidosaurs

Table 2 Descriptive statistics of the species means of all noningestion chewing cycles

Species	Data source	Individuals (n)	Foods	Cycles (n)	Mean cycle length (ms)	CV
Lepidosaurs						
Oplurus cuvieri	(Delheusy and Bels 1992)	4	Adult live crickets	100	232.00	48.28
Chamaeleo jacksonii	(So et al. 1992)	3		15	1266.21	27.86
Agama stellio	(Herrel et al. 1997)	4	Grasshoppers	172	883.02	68.64
Corucia zebrata	(Herrel et al. 1999)	2	Endive, apple, tomato, banana	135	338.96	46.53
Pogona vitticeps	(Metzger 2005)	5	Beetle, cricket, field cricket, locust	1578	241.20	108.76
Tiliqua rugosa	(Metzger 2005)	2	Beetle, cricket, field cricket, locust, baby mouse	83	442.41	23.24
Tiliqua scincoides	(Metzger 2005)	4	Beetle, cricket, field cricket, locust, baby mouse	1263	576.59	33.99
Tupinambis merianae	(Metzger 2005)	2	Cricket, field cricket, locust, baby mouse	753	490.11	41.58
Uromastix acanthinurus	(Herrel and De Vree 1999)	2	Endive, locusts	69	713.04	41.91
Varanus niloticus	(Metzger 2005)	3	Baby mouse	467	669.70	193.19
Phelsuma madagascariensis	Herrel, unpublished	1		61	1036.92	52.40
Cordylus tropidosternon	Herrel, unpublished	1		16	1166.25	37.21
Sphenodon punctatus (*adult*)	(Gorniak et al. 1982)	3	Crickets, cockroaches, juvenile mice	235	807.18	21.12
Sphenodon punctatus (*juv*)	Schaerlaeken, Herrel, Ross, unpublished	3	Mealworm, waxworm, beetle	155	1151.28	70.26
Mammals						
Allenopithecus nigroviridis	Lincoln Park Zoo	3	Chow, lettuce	264	476.75	30.71
Llama pacos	(Williams 2004)	4	Hay	136	562.67	24.27
Aotus trivirgatus	Ross and Hylander (2000)	3	Apple, gummy bear, prune, carrot, plantains, apricot	789	395.63	30.81
Callithrix geoffroyi	Brookfield Zoo	1	Fruit, egg	84	337.46	19.34
Capra capra	(Williams 2004)	2	Hay	89	625.88	11.00
Cheirogaleus medius	DULC	3	Pear, meal worm, chow	261	234.16	18.68
Chlorocebus aethiops	Ross, unpublished	1	Grape, prune, apple, almond	222	387.93	23.17
Colobus guereza	Lincoln Park Zoo	2	Carrot, chow	147	422.04	25.37
Daubentonia madagascariensis	DULC	3	Orange, corn	112	323.52	23.23
Cercopitheus neglectus	Lincoln Park Zoo	1	Chow	101	484.54	25.63
Equus caballus	(Williams 2004)	2	Hay	98	773.52	14.69
Eulemur fulvus	Ross, unpublished	3	Apple, grape, raisin	551	308.49	21.56
Eulemur coronatus	DULC	3	Apple, melon	83	215.10	12.76
Eulemur fulvus albifrons	DULC	1	Pears, lettuce, grapes	78	243.27	16.95
Eulemur fulvus sanfordi	DULC	3	Sweet potato, apple	119	199.66	17.72
Eulemur mongoz	DULC	2	Apple, pear, chow	142	213.57	20.71
Galago moholi	DULC	1	Mealworm	43	240.21	21.89
Gorilla gorilla	Lincoln Park Zoo	1	Lettuce, carrot	161	616.96	20.17
Hapalemur griseus	DULC	1	Sweet potato	41	292.98	18.71
Hylobates lar	Lincoln Park Zoo	2	Lettuce	92	326.41	16.72
Lemur catta	DULC	3	Pear, chow	105	250.49	18.33

(Continued)

Table 2 (Continued)

Species	Data source	Individuals (n)	Foods	Cycles (n)	Mean cycle length (ms)	CV
Loris tardigradus	DULC	1	Mealworm	27	471.78	17.22
Macaca mulatta	Ross, unpublished	3	Grape, apple, jaw breaker, taffy, apricot, prune, almond	367	729.53	21.97
Mandrillus sphinx	Lincoln Park Zoo	4	Chow	238	601.76	28.26
Microcebus murinus	DULC	3	Mealworm, grape	46	205.89	15.18
Nycticebus coucang	DULC	2	Fruit, grape	27	389.89	15.40
Nycticebus pygmaeus	DULC	2	Fruit, grape	89	381.91	15.07
Otolemur crassicaudatus	Ross, unpublished	2	Grape, apple, gummy bear, raisin	64	511.77	18.71
Pan troglodytes	Lincoln Park Zoo	1	Lettuce	45	495.00	17.06
Pithecia pithecia	Lincoln Park Zoo	2	Chow, carrot	278	380.21	23.32
Propithecus tattersalli	DULC	1	Carrot, chickpeas, corn, greens	54	269.50	14.02
Propithecus verreauxi	DULC	1	Carrot, chickpeas, corn, greens	127	252.05	17.89
Saguinus fuscicollis	Brookfield Zoo	1	Chow	12	313.50	13.09
Varecia variegata rubra	Ross, unpublished	4	Apple, grape, raisin	398	317.15	21.09
Tupaia glis	(Fish and Mendel 1982)	5	Almond, chow, mealworm	444	291.25	16.85
Oryctolagus cuniculus	(Yamada and Yamamura 1996)	9	Bread, pellet, rice	69	252.33	10.83
Tenrec ecaudatus	(Oron and Crompton 1985)	1	Ground meat, chicken flesh, chicken bone	69	378.09	16.07
Pteropus giganteus	(De Gueldre and De Vree 1984)	15	Banana, apple, soaked raisin	69	597.07	15.11
Suncus murinus	(Dötsch 1986)	9	Mealworm, cricket	273	183.00	22.95
Pedetes capensis	(Offermans and De Vree 1990)	2	Rolled oats, ground nut, maize	128	319.83	8.30
Felis catus	(Thexton et al. 1980)	5	liver, varied hardness and size		341.75	16.54
Didelphis virginiana	(Hiiemae and Crompton 1971)		Chicken leg or wing, chicken bone, dog food	332	214.93	12.82
Homo sapiens	(Hiiemae et al. 1996)	11	Apple, banana, cookie	1054	667.15	21.92
Tupaia glis	(Hiiemae and Kay 1973)	?		111	244.53	13.74
Otolemur crassicaudatus	(Hiiemae and Kay 1973)	?		94	312.11	15.72
Saimiri sciureus	(Hiiemae and Kay 1973)	?		104	350.50	19.76
Ateles sp.	(Hiiemae and Kay 1973)	?		100	324.48	18.18

Notes: References refer to papers from which data were obtained. Data from Thexton et al. (1980) were obtained by digitizing Fig. 3. Where names of authors of this article are given without a date, the data are previously unpublished and were taken from data files recorded in our laboratories. DULC = Duke University Lemur Center.

because mammals presumably use their feeding system more than do lepidosaurs. In contrast with mammals, the lizards sampled for this study do not show a negative relationship between chew frequency (the inverse of cycle length) and jaw length. The sample of lizards does not extend across the size range of the mammals, but nevertheless, the absence of a size-related change is notable. One possible explanation for this is that the lower energy requirements of lizards mean that they do not use their feeding system in a rhythmic manner for long enough periods of time for optimization of energy consumption to be a constraint on cycle length.

The evolution of rhythmic chewing, periodontal afferents, and the fusimotor system

It was argued in the Introduction that mammalian chewing should be modulated to provide improved temporal and energetic efficiency relative to non-mammals, thereby meeting the higher rates of food intake demanded by the elevated metabolic rates of mammals. It was suggested that by minimizing the

Table 3 Mean cycle length, body mass, and lower jaw length for lepidosaur species sampled for this study

Genus	Species	Mass (g)	Snout-vent length (mm)	Lower jaw length (mm)	Cycle length (s)
Anolis	carolinensis	4.89	61.56	20.52	0.66
Anolis	sagrei	4.66	55.4	15.26	0.72
Cnemidophorus	burti	40.39	108.75	29.36	0.59
Cnemidophorus	Uniparens	2.83	51.51	13.03	0.49
Cnemidophorus	velox	11.06	73.59	19.21	0.6
Cnemidophorus	tigris	8.7	70.18	18.87	0.4
Coleonyx	brevis	3.82	61.47	13.58	1.3
Corucia	zebrata	620	290	56	0.34
Crotaphytus	collaris	37.2	98.56	30.14	0.8
Dipsosaurus	dorsalis	49.17	111.02	21.53	0.55
Eublepharis	macularius	17.1	124.31	17.1	0.45
Eumeces	fasciata	2.08	67.23	12.37	1.33
Gambelia	wislizenii	18.56	100.84	27.75	0.55
Gekko	gecko	30.8	131.02	30.8	1
Gherronotus	kingii	11.44	83.29	17.28	1.55
Holbrookia	maculata	3.87	52.68	11.82	0.74
Ophisaurus	ventralis		270	34.74	4.41
Phelsuma	madagascariensis	15.8	96.74	26.37	1.64
Plocederma	stellio	42	20	32	0.9
Pogona	vitticeps	237.908	176.604	49.98	0.241
Sceloporus	clarckii	33.03	102.73	24.36	0.88
Sceloporus	grammicus		68.57	16.29	0.66
Sceloporus	magister		97.28	23.61	0.42
Sceloporus	olivaceus		93.93	23.21	0.61
Sceloporus	poinsetti		87.59	22.17	0.65
Sceloporus	serrifer		92.32	23.4	0.55
Sceloporus	undulatus	10.69	68.31	16.22	0.7
Tiliqua	rugosa	284.41	471	52.1	0.442
Tiliqua	scincoides	272.15	381.01	52.19	0.577
Tupinambis	merrianae	358	2048	90.14	0.49
Tupinambis	teguixin		328	70	0.59
Uromastix	acanthinurus	141	162	34.5	0.713
Uromastix	aegyptia		600		0.61
Urosaurus	ornatus	3.1	50.03	12	0.86
Varanus	exanthematicus		243	60	0.48
Varanus	niloticus	363	888	71.22	0.67
Varanus	ornatus	415	1578	85.29	0.51
Sphenodon	punctatus	24.027			1.03038

variance of cycle length around the natural frequency of the feeding system, the mammalian chewing system can operate for longer without fatigue, thereby facilitating more intra-oral processing per food item, and longer feeding bouts overall. Here we argue that two specific modifications to the sensorimotor components of the mammalian feeding system facilitate this decreased variance of cycle length: periodontal afferents and fusimotor efferents to muscle spindles (Fig. 7).

Periodontal afferents are an important source of sensory information that mammals use to modulate
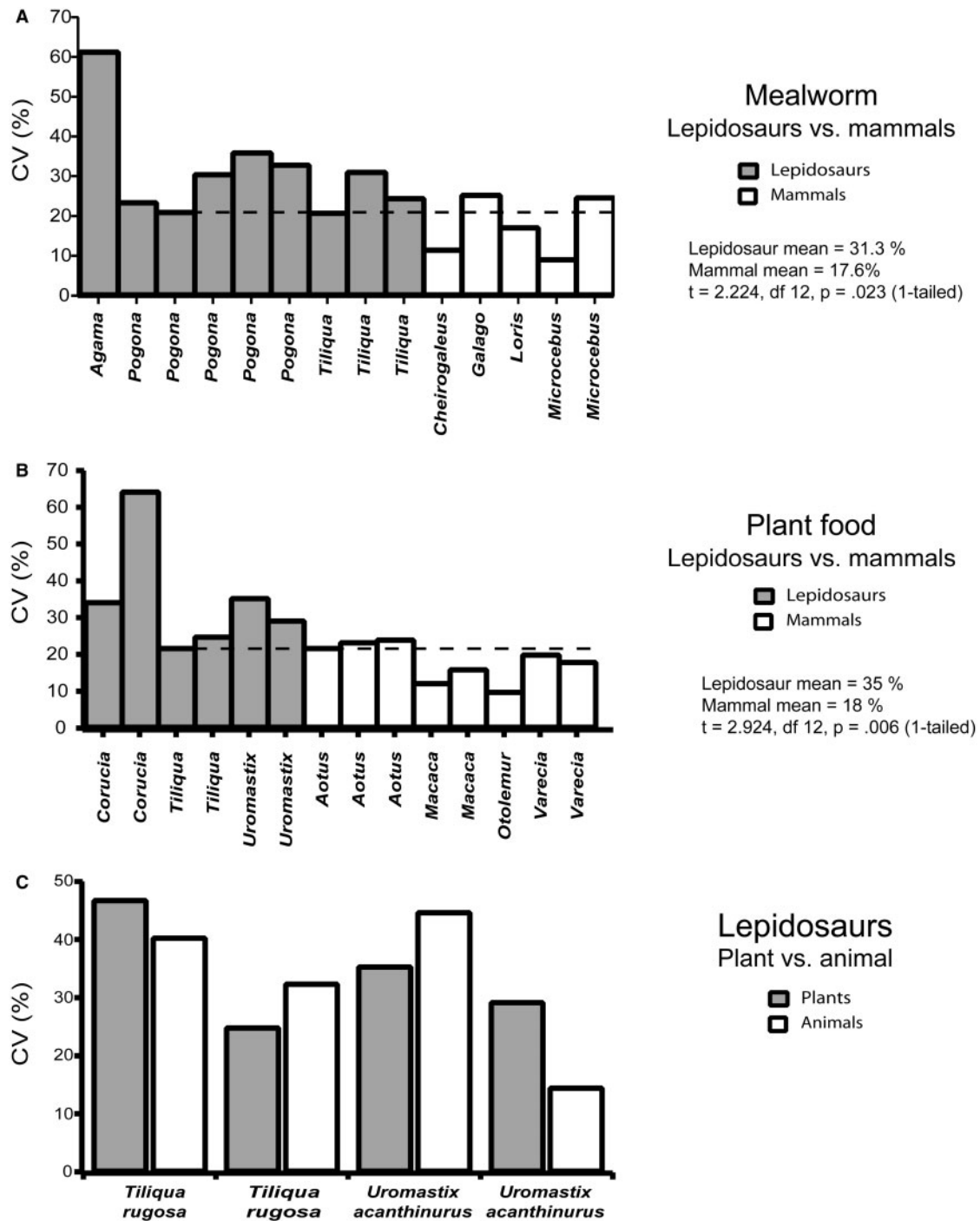
Fig. 6 (**A**) Histogram of CV$_i$s (standard deviation expressed as a percentage of mean cycle length within each individual) for individual lepidosaurs and mammals calculated from all sequences in which mealworms were eaten. Mean for lepidosaurs = 31.3%; Mean for mammals = 17.6%; $t = 2.224$, df 12, $P = 0.023$ (1-tailed). Mammals have lower CV$_i$s than do lizards. The dashed line lies at the level of the CV of two lizards with lower CVs than two of the mammals sampled. (**B**) Histogram of CV$_i$s (standard deviation expressed as a percentage of mean cycle length within each individual) for individual lepidosaurs and mammals calculated from complete sequences in which plant food was eaten. Mean for lepidosaurs = 35%; Mean for mammals = 18%; $t = 2.924$, df 12, $P = 0.006$ (1-tailed). Mammals have lower CV$_i$s than do lizards when only plant-eating cycles are considered. The dashed line lies at the level of the CV of one lizard with a lower CV than two of the mammals sampled. (**C**) Bar plot of mean CVs calculated within four individual lizards that ate both plants and animals. There is no consistent pattern for food cycles to be less variable when plants were eaten than when animals were consumed.
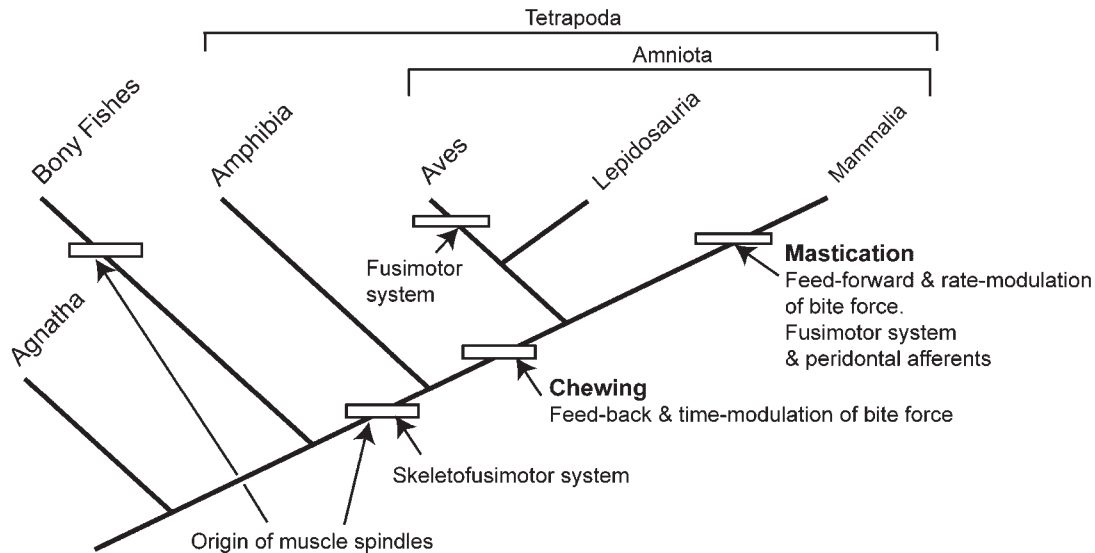
Fig. 7 Phylogeny outlining the evolution of intra-oral processing, muscle spindles, fusimotor efferents, skeletofusimotor efferents, and periodontal afferents in vertebrates (Maeda et al. 1983; Reilly and Lauder 1990; Crowe 1992; Reilly et al. 2001; Ross et al. 2007). Muscle spindles are absent in agnathans and have only been reported in one fish (from the jaw adductors in *Salmo*) (Maeda et al. 1983) and are not, to our knowledge, found in locomotor muscles of fish. Pending further evidence, we hypothesize that spindles evolved independently in basal tetrapods and in some fish. Turtle spindles are well studied, those of lepidosaurs less so, but evidence for γ-motoneurons is lacking in both groups (Crowe 1992). Muscle spindles are known to be widely distributed in the flight, leg, and jaw muscles of birds; morphological evidence for the presence of β-motoneurons and γ-motoneurons has been reported in birds, but their physiological properties and role in modulation of rhythmic movements are unstudied (Maier 1992a, 1992b). We hypothesize that the fusimotor systems of birds and mammals evolved independently.

intra-oral food processing. These afferents apparently evolved convergently in mammals and crocodilians (Mcintosh et al. 2002). Periodontal receptors are unencapsulated Ruffini-type endings that encode information on the orientation, magnitude, rate, and position of loads applied to the teeth (Hannam 1969; Hannam and Farnsworth 1977; Larson et al. 1981; Byers 1985; Loescher and Robinson 1989; Johnsen and Trulsson 2003, 2005). A few periodontal receptors show linear responses into higher force ranges, but most are slowly adapting, saturate at relatively low force levels, and show peak levels of activity at tooth-food-tooth contact at the start of the power stroke (Appenteng et al. 1982; Johnsen and Trulsson 2005; Trulsson 2006). Thus, periodontal receptors "are well suited to encode in detail the temporal changes in the chewing force that occur during the early contact phase of each chewing cycle" (Trulsson, 2006: 271). Information from periodontal afferents is used in feed-back modulation of jaw movements and bite force via reflex behaviors that protect the teeth (Türker and Jenkins 2000; Türker 2002) and in the feed-forward or anticipatory modulation of masticatory force (Komuro et al. 2001a, 2001b; Ottenhoff et al. 1992a, 1992b).

Muscle spindles are encapsulated sensory receptors in tetrapod muscles that register change in length and, in some cases, rate of change in length of their host muscles through primary (Ia) and secondary (II) afferents. The sensory receptors are modified muscle fibers called intrafusal fibers, separated from the rest of the muscle (extrafusal fibers) by a capsule. In addition to sending afferent fibers into the brainstem, the muscle spindles of tetrapods also receive efferent innervation. All tetrapods so far studied possess β-motoneuron efferents to the intrafusal fibers, collaterals of the α-motoneurons to the extrafusal muscle fibers. These β-motoneurons form the efferent limb of what is termed the *skeletofusimotor* system, a mechanism found throughout tetrapods (Fig. 7). These efferents go to the nonsensory, contractile portions at the end of the intrafusal fibers and function in maintaining tension, and hence some responsiveness in the spindle as the muscle shortens. In addition to this skeletofusimotor system, mammalian intrafusal muscle fibers also receive γ-motoneurons, the efferent limb of the *fusimotor* system found only in mammals (Crowe 1992). The *fusimotor system* modulates the response properties of the muscle spindles, enabling spindle output to be tuned to different motor tasks, in effect

changing the functional "set" of the feeding system (Prochazka et al. 1988). This makes the fusimotor system of special importance in studies of modulation.

Mammalian muscle spindles perform a number of tasks related to modulation of intra-oral transport and food processing. Along with periodontal afferents, muscle spindles play an important role in regulating masticatory force (Hidaka et al. 1997, 1999) and they monitor the timing of both maximal jaw opening and the start of the power stroke during natural chewing (Taylor and Davey 1968; Taylor and Cody 1974; Cody et al. 1975; Goodwin and Luschei 1975; Lund et al. 1979). The response properties of muscle spindles are themselves modulated according to the stage in the chewing sequence (Masuda et al. 1997) and they provide direct input to neurons in the brainstem thought to form part of the CPG for mastication (Tsuboi et al. 2003) and to parts of the sensorimotor cortex thought to modulate chewing. Although the functional role of the fusimotor system during mastication is not well studied in awake, alert animals, several lines of evidence suggest that mammals utilize their novel fusimotor system in *anticipatory*, or *feed-forward* modulation of chewing behavior.

First, both the dynamic and the static efferents of the fusimotor system function in an anticipatory capacity: the former acts tonically during jaw movements to adjust the sensitivity of primary afferents to changing stretch in the jaw muscles, whereas the static fusimotor system acts phasically to provide a template of the temporal characteristics of intended movement (Appenteng et al. 1980; Gottlieb and Taylor 1983). Second, muscle spindle afferents also appear to be important in modulating the temporal aspect of anticipatory feed-forward control (whereas the periodontal afferents modulate its amplitude) (Komuro et al. 2001a, 2001b). This anticipatory control is evident in amplitudes in activity of the masseter muscle that are modulated in an anticipatory manner during cortically-evoked rhythmic jaw movements (CRJMs): i.e., when a hard test strip is placed between the molars during one chewing cycle, masseter muscle activity is facilitated in subsequent cycles *prior to* generation of masticatory force. Whereas the *amplitude* of this anticipatory response is mediated by periodontal afferents, the *temporal* component is modulated via spindle afferents (Komuro et al. 2001a, 2001b). Finally, it has been shown that in naturally behaving cats, the nature and level of activity in γ-motoneurons varies with task and context, and that activity levels in both static and dynamic γ-motoneurons increase with the

speed and difficulty of the task (Prochazka et al. 1988). Although the latter study focused on the locomotor system, some data suggest a similar role for γ-motoneurons in the masticatory system of cats and primates (Cody et al. 1975; Lund et al. 1979; Taylor et al. 1981). Together, the evidence presented above suggests that the fusimotor system in mammals is a component of a feed-forward system that modulates spindle sensitivity and mediates anticipatory control of jaw muscle activity and bite force.

The ability to feed-forward information from one bite to the next has the advantage of enabling motor commands to be sent out to the jaw muscles that are appropriate for the material properties of the food before the teeth make contact with the food. In this way, jaw-closing velocity can be kept relatively constant as the teeth come into contact with food at the start of the slow close/power stroke phase, dampening the effects of the change in external forces acting on the mandible (Wang and Stohler 1991; Ottenhoff et al. 1992a, 1992b, 1996; Abbink et al. 1999). We hypothesize that this dampening effect allows chewing to proceed at a relatively constant rate because it minimizes variation in cycle length due to variation in material properties of the food both within and between chewing sequences. The hypothesis that mammals use feed-forward control of bite force to minimize variance of cycle length accords well with data we have published elsewhere demonstrating that mammals modulate bite force predominantly by varying the rate at which force is generated during a chewing cycle, rather then by varying the time over which it is generated (Ross et al. 2007). This strategy enables mammals to minimize variation in cycle length despite variation in both material properties of the food and the various functions, such as processing and transport, that can occur in a single cycle. Whether lizards also display rate-modulation rather than time-modulation of bite force has yet to be determined. Work currently in progress will address this issue.

If the hypothesis presented here is correct—that the fusimotor system improves chewing efficiency in mammals by minimizing the variance of cycle length—and if this improved efficiency increases stamina of the chewing system, then endothermic vertebrates in general can be predicted to utilize fusimotor systems to modulate cycle length in repetitive, cyclic behaviors in which feed-forward modulation of force improves performance. Such behaviors include locomotion under conditions when substrate reaction forces are variable, but which can be predicted based on afferent information acquired

during preceding steps. Mammalian locomotion is known to take advantage of fusimotor systems to alter the functional "set" of the limb muscles (Prochazka et al. 1976, 1988), and birds are thought to possess neurons comparable to the γ-moto-neurons of mammals (Maier 1992a, 1992b). Comparisons of variances in cycle length of avian and mammalian locomotion with that in other amniote vertebrates possessing only a skeletofusimotor system (e.g., turtles and crocodiles) are being pursued to test this hypothesis.

Conclusions

We hypothesize that the decreased cycle lengths and decreased variance in cycle lengths in mammals compared with lizards allow more rapid intra-oral processing of food for longer periods of time without fatigue. Both of these factors would improve feeding performance in mammals compared with lizards, facilitating the higher rates of energy intake needed to fuel their elevated metabolism. Our hypothesis is that the decreased cycle lengths and decreased variance in cycle lengths in mammals were made possible by the evolution of fusimotor innervation of muscle spindles and periodontal afferents, which provided the substrate for feed-forward control. These improved modulatory abilities join the evolution of precise occlusion, diphyodonty, and a transverse component to the power stroke that currently distinguishes mammalian mastication from the intra-oral processing of other vertebrates.

Although the term *mastication* should be reserved for the chewing behavior of mammals, it is important to realize that many nonmammalian vertebrates "chew", or perform cyclic intra-oral food processing, (Schwenk 2000a, 2000b; Reilly et al. 2001). We view mammalian mastication as an extreme on a continuum of intra-oral food-processing behaviors, ranging from opportunistic application of force by the jaws or tongue during transport cycles, through the irregular chewing cycles of nonmammals (Smith 1982; So et al. 1992), to the highly integrated, rhythmic and repetitive mastication of mammals in which chewing and transport can occur in the same cycle (Schwenk 2000a, 2000b). We argue that the degree to which the continuum of intra-oral processing can be non-arbitrarily partitioned depends in part on whether *chewing* and *mastication* employ novel sensorimotor systems for modulation. The data presented here suggest that mammalian mastication is in part dependent on novel modulatory mechanisms, and the evolution of those mechanisms serves to place the food-processing continuum in a meaningful, evolutionary context.

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