

Modulation of mandibular loading and bite force in mammals during mastication

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Accepted 25 January 2007

Summary

Modulation of force during mammalian mastication provides insight into force modulation in rhythmic, cyclic behaviors. This study uses *in vivo* bone strain data from the mandibular corpus to test two hypotheses regarding bite force modulation during rhythmic mastication in mammals: (1) that bite force is modulated by varying the duration of force production, or (2) that bite force is modulated by varying the rate at which force is produced. The data sample consists of rosette strain data from 40 experiments on 11 species of mammals, including six primate genera and four nonprimate species: goats, pigs, horses and alpacas. Bivariate correlation and multiple regression methods are used to assess relationships between maximum (ϵ_1) and minimum (ϵ_2) principal strain magnitudes and the following variables: loading time and mean loading rate from 5% of peak to peak strain, unloading time and mean unloading rate from peak to 5% of peak strain, chew cycle duration, and chew duty factor. Bivariate correlations reveal that in the majority of experiments strain magnitudes are significantly ($P < 0.001$) correlated with strain loading and unloading rates and not

with strain loading and unloading times. In those cases when strain magnitudes are also correlated with loading times, strain magnitudes are more highly correlated with loading rate than loading time. Multiple regression analyses reveal that variation in strain magnitude is best explained by variation in loading rate. Loading time and related temporal variables (such as overall chew cycle time and chew duty factor) do not explain significant amounts of additional variance. Few and only weak correlations were found between strain magnitude and chew cycle time and chew duty factor. These data suggest that bite force modulation during rhythmic mastication in mammals is mainly achieved by modulating the rate at which force is generated within a chew cycle, and less so by varying temporal parameters. Rate modulation rather than time modulation may allow rhythmic mastication to proceed at a relatively constant frequency, simplifying motor control computation.

Key words: bone strain, muscle recruitment, size principle, chewing.

Introduction

Mammalian mastication is a rhythmic, cyclic activity, the rhythmic components of which are controlled by at least one central pattern generator located in the lateral reticular formation in the brainstem or the principal sensory nucleus of the trigeminal (Lund et al., 1998; Tsuboi et al., 2003; Westberg et al., 2001). To facilitate effective occlusion without damaging the teeth, masticatory movements and forces must be adjusted in response to variation in material properties of the food, between and within chewing sequences and cycles (Agrawal et al., 2000; Ahlgren, 1976; Anderson et al., 2002; Blanksma and Van Eijden, 1995; Ottenhoff et al., 1993; Ottenhoff et al., 1992;

Ottenhoff et al., 1996; Peyron et al., 2002; Proschel and Hofmann, 1988). This active adjustment of movement and force by the central nervous system (CNS) in response to variation in some external variable is referred to here as modulation (Deban et al., 2001; Herrel et al., 2001). Evidence of modulation is usually derived from systematic covariation between external variables (e.g. sex of the subject, material properties of foods or objects placed between the teeth, external forces applied to the system) and the behavior of the subject, as quantified by kinematic or electromyographic variables (Anderson et al., 2002; Buschang et al., 2000; Hidaka et al., 1997; Lavigne et al., 1987; Lund et al., 1998; Morimoto et al.,

1989; Nakajima et al., 2001). These studies reveal that descending control and afferent information from muscle spindles, Golgi tendon organs, and stretch receptors in the periodontal and 'periarticular' ligaments modulate the motor program and temporal and spatial patterns of jaw movement (Sessle, 2006).

Modulation of the magnitude and orientation of the bite force is less well documented, primarily because bite force is difficult to measure directly *in vivo* during mastication. Some workers have related variation in EMG patterns to variation in bite force orientation and magnitude during isometric biting on a bite force transducer (Blanksma et al., 1997); others have measured bite force orientations and/or magnitudes from intra-oral implants in edentulous (Mericske-Stern et al., 1992) or partially dentate (Lundgren and Laurell, 1986) subjects. These studies have various limitations, the most serious of which is destruction of the periodontal ligament afferents employed to modulate bite force production (Trulsson, 2006).

An alternative method for investigating bite force modulation is to use bone strain from the mandibular corpus below the molar teeth as an indirect estimate of changes in bite force (Hylander, 1977; Hylander, 1986; Weijs and De Jong, 1977). This method has the advantage of being easy to apply to a wide range of animals without significantly impacting normal masticatory function. Empirical support for the relationship between bite force and mandibular bone strain comes from Hylander's investigation of mandibular corpus bone strain data during isometric biting on a force transducer (Hylander, 1977; Hylander, 1979; Hylander, 1986). Hylander reports "*that when bite-point position is held constant, there is a high positive correlation between the magnitude of peak bite force and peak mandibular bone strain during isometric biting in both macaques and galagos*", concluding that "*bone-strain patterns along the working side of the mandible are a good indicator of bite-force patterns during the power stroke*" [Hylander (Hylander, 1986), p. 149]. These data suggest that mandibular corpus bone strain data may provide insight into modulation of bite force during mastication in mammals (Weijs and De Jong, 1977, p. 647).

Hypotheses

The primary aim of this study is to determine how bite force is modulated during rhythmic mastication in mammals. Because patterns and mechanisms of force modulation also impact other temporal aspects of chewing cycle dynamics, the relationship between corpus bone strain magnitude – a proxy for bite force – and both chewing cycle duration and chewing 'duty factor' are also evaluated (where duty factor is the percentage of the chewing cycle over which the jaw is loaded). Specifically, the present study used bone strain data from a range of mammals to examine how strain magnitude in the mandibular corpus and, by inference, bite force, are related to the loading and unloading rates, loading and unloading times, overall chew cycle time, and chewing 'duty factor'.

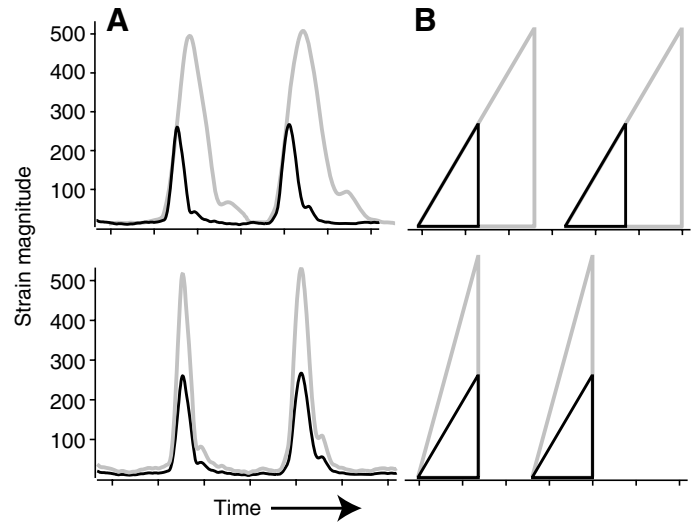


Fig. 1. Diagram illustrating two ways of modulating strain magnitude and bite force during the power stroke of a chewing cycle. (A) Strain profiles, modified to illustrate the hypotheses. (B) Triangles illustrating the variables measured in this study. Note that these triangles only describe strain profiles in loading (i.e. prior to peak strain). The dark lines and triangle are low-magnitude events, while the lighter (red) lines are higher-magnitude events. (Top) Magnitude can be increased by increasing loading time, while load rate is kept constant. (Bottom) Magnitude can be increased by increasing loading rate, while keeping loading duration constant. Combinations of these strategies are possible.

The possible relationships between strain magnitude, and loading time and rate are easily understood by modeling the loading portions of the strain profile as a triangle, with strain magnitude represented by the vertical limb of the triangle, loading time by the base, and loading rate as strain magnitude/loading time (Fig. 1).

Strain magnitude can be increased by increasing loading time while maintaining a constant load rate (top row, Fig. 1), increasing load rate while maintaining a constant load time (bottom row, Fig. 1), or some combination of the two. If strain magnitude is increased by increasing loading time (i.e. time-modulated), then either chewing duty factor must increase, overall cycle time must increase (i.e. chewing frequency must decrease), or both. This hypothesis predicts that variation in strain magnitude will be positively correlated with variation in load time, will not be correlated with strain rate, and will be correlated with increases in chewing duty factor and cycle time. Empirical support for this hypothesis derives from studies demonstrating that increases in hardness of objects placed between the teeth during cortically evoked rhythmic jaw movements (CRJMs) are associated with increases in cycle time (Hidaka et al., 1997; Lavigne et al., 1987; Liu et al., 1998; Liu et al., 1993). Time-modulation of force is also suggested by data showing that when harder foods are chewed there are increases in cycle time, increases in the duration of the slow close or power stroke phase of the chewing cycle, and/or increases in burst durations of jaw adductor muscles (Kakizaki

et al., 2002; Weijs and Dantuma, 1981; Yamada and Haraguchi, 1995; Yamada and Yamamura, 1996).

If strain magnitude is increased by increasing load rate without increasing load time (i.e. rate-modulated), cycle time will remain relatively constant and there need not be changes in cycle time or duty factor. This hypothesis predicts that variation in strain magnitude will be positively correlated with variation in strain rate, and not with variation in load time, chewing duty factor, or cycle time. Theoretical support for this hypothesis derives from considerations of the consequences of orderly recruitment of motor units, the primary mechanism for force modulation at low force amplitudes during mastication (Goldberg and Derfler, 1977; Hannam and McMillan, 1994; Scutter and Türker, 1998) and locomotion (Fournier and Sieck, 1988; Hennig and Lomo, 1987; Tansey et al., 1996). If the small motor neurons, which innervate small motor units consisting of slow twitch fibers, are recruited first, followed by progressively larger motor neurons and motor units consisting of faster fiber types, then increases in bite force will necessarily be achieved in a constant or decreasing time period. The evidence for the orderly recruitment of motor units during mastication is summarized in the Discussion. Weijs and DeJongh have presented empirical support for this hypothesis (Weijs and DeJongh, 1977), and their data show that differences in strain magnitudes when chewing different foods are accounted for by differences in strain rate. In addition, their EMG data (Weijs and Dantuma, 1981) reveal that increases in vertical components of jaw elevator muscle force are achieved via increases in rate of force development.

While modulation of bite force and correlated changes in bone strain magnitudes during the loading portion of the chewing cycle is to be expected in theory and is suggested empirically, it is less clear that modulation during the unloading portion of the chewing cycle will be functionally related to bite force modulation. Muscles acting to move the teeth out of occlusion (e.g., balancing side deep masseter) and open the jaws (digastric, mylohyoid, geniohyoid) do strain the mandible after centric occlusion, and modulation of mandibular loading might be expected in relation to these forces. However, strain during unloading of the mandible is thought to be primarily affected by the relaxation characteristics of the jaw elevator muscles (Hylander and Johnson, 1993; Hylander and Johnson, 1994; Hylander et al., 1987; Luschei and Goodwin, 1974).

Materials and methods

Data sample

The mandibular bone strain data analyzed for this study (Table 1) were recorded in three different laboratories in connection with other studies (Herring and Teng, 2000; Hylander et al., 1998; Liu et al., 2004; Liu and Herring, 2000a; Liu and Herring, 2000b; Rafferty, 2005; Ravosa et al., 2000; Ross and Hylander, 1996; Thomason et al., 2001; Williams, 2004). Data were available for 3084 chewing cycles from 31 individuals of 11 species, including seven species of primates (four anthropoid and three strepsirrhine species), as well as

goats (*Capra*), horses (*Equus caballus*), alpacas (*Lama pacos*), and miniature pigs (*Sus*) (Table 1). The data were collected in 40 experimental sessions, referred to hereafter as 'experiments'. Data were collected from four of the primate subjects in two separate experiments.

The data were collected with either delta or rectangular rosette strain gages. Gage location varied between experiments, although all the data discussed here were collected from the lateral aspect of the mandibular corpus below the molars or premolars. Some gages were placed close to the lower (ventral) border of the mandibular corpus, others at mid-corpus height (Table 1). The gages were placed on the mandibular corpora with the animals under sedation with ketamine (primates at Duke University); or anesthesia with isoflurane (primates at Stony Brook University); isoflurane and nitrous oxide (goats at University of Washington); 5 mg kg⁻¹ ketamine, 0.05 mg kg⁻¹ butorphenol, 0.5 mg kg⁻¹ xylazine intramuscularly (IM) (alpacas at Duke University); medetomidine 0.03-0.05 mg kg⁻¹ IM reversed with atipamezole IM (goats at Duke University); or halothane and nitrous oxide (pigs at University of Washington). The horses at Duke University were tranquilized with 1.1 ml kg⁻¹ xylazine intravenously (IV), anesthetized with 2.0 ml kg⁻¹ ketamine IV, and an additional 2.0 ml kg⁻¹ ketamine administered IV every 10-15 min, as needed (Riebold et al., 1995).

The periosteum was scraped away from the gage sites, the bone degreased, and the gages bonded to the bone using cyanoacrylate adhesive. The lead wires were run out through the incision sites, which were sutured closed. The gage elements were connected to standard strain amplifiers, i.e. as one arm of a Wheatstone bridge, and the elements calibrated using shunt calibrations. Various other kinds of data were often recorded simultaneously, such as electromyographic data, or strain data from other sites, but these data are not discussed here.

After the animals recovered from anesthesia, strain data were recorded the same day. The animals were presented with a range of food types, depending on the species (Table 1). Data were either recorded on analog tape and digitized later using A/D boards in personal computers (e.g. data from the Hylander laboratory at Duke University), or digitally recorded directly to computer (data from the Ross and Herring laboratories). The digitizing frequencies are given in Table 1. Using the calibration files, the raw data files were converted to microstrain. The rosette data were used to calculate magnitudes and orientations of principal strains. Strain (ϵ), a dimensionless unit equaling the change in length of an object divided by its original length, is measured in microstrain ($\mu\epsilon$) units that are equal to 1×10^{-6} strain. Tensile strain is registered as a positive value, and compressive strain as a negative value. The maximum principal strain (ϵ_1) is usually the largest tensile strain value, while the minimum principal strain is usually the largest compressive strain value (ϵ_2).

The principal strain values were imported into IGOR Pro 4.0 (WaveMetrics, Lake Oswego, OR, USA) where the following variables were extracted from each chewing cycle (see Fig. 2):

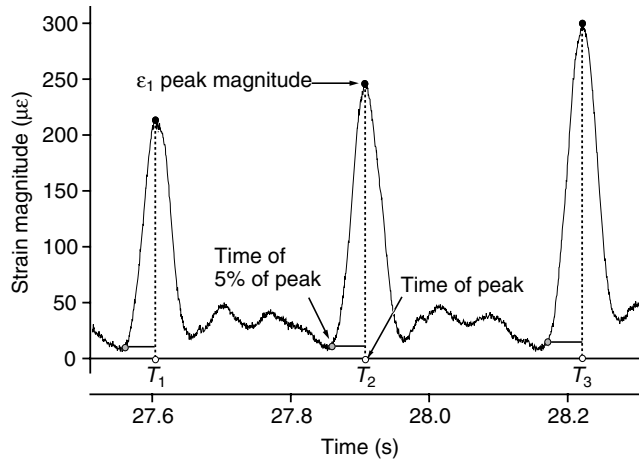


Fig. 2. Illustration of variables extracted from the strain data. Plot of ϵ_1 magnitude recorded from lateral aspect of the mandibular corpus of owl monkey 1 in experiment 9 (data from C.F.R. and W.L.H., recorded at Duke University). Three chews ipsilateral to the strain gage are shown. The strain profile between power strokes does not return to zero because of strain in the mandible during opening. The following data were extracted from each power stroke: time (open circles) and magnitude (black circles) of peak strain, and time at which 5% of peak strain was reached in loading (grey circles). The duration of loading was calculated as the time from 5% of peak to strain to peak strain; the loading rate was calculated as peak strain magnitude divided by duration of loading. Cycle time for each cycle was estimated as the duration of time from the preceding peak to the following peak, divided by 2. In the case of the middle cycle in this figure, cycle time = $(T_3 - T_1)/2$.

- (1) Peak strain magnitude: the magnitude of the largest values of ϵ_1 and ϵ_2 during the closing stroke;
- (2) Peak strain timing: the time at which peak strain magnitudes (ϵ_1 and ϵ_2) were reached;
- (3) 5% timing: the time at which 5% of peak strain magnitude was reached in loading and unloading;
- (4) Load time: the amount of time between 5% of peak strain in loading and peak strain;
- (5) Cycle time: the duration of the chewing cycle, estimated as the average of the times from the preceding peak to the current peak, and from the current peak to the following peak;
- (6) Unload time: the amount of time between peak strain and 5% of peak in unloading;
- (7) Standardized load time (load time STD): load times expressed as a percentage of overall cycle time;
- (8) Duty factor: total load time as a percentage of chewing cycle time, i.e. the percentage of the cycle during which the mandible is loaded;
- (9) Load rate: for each chew cycle, the average loading rate between 5% of peak and peak, i.e. $\delta y/\delta x$, where δy = peak magnitude and δx = load time
- (10) Unload rate: for each chew cycle, the average unloading rate between peak strain and 5% of peak strain, i.e. $\delta y/\delta x$, where δy = peak magnitude and δx = unload time

The duration of loading, unloading, loading rate and

unloading rate are measured from the first occurrence of 5% of peak, rather than zero, strain in each power stroke because the strain profile often does not drop to zero between the strain associated with the opening phase and that associated with closing. These strains are particularly prevalent in taxa that chew rapidly and experience significant corpus strains during jaw opening (e.g. Fig. 2).

Ingestion cycles (cycles in which food is brought into the mouth) were excluded and data were only included from chewing cycles in which the animals chewed ipsilateral to the corpus strain gages; i.e. only working side bone strain data are examined here. Chewing side was determined using EMG patterns and/or jaw kinematic data. Chewing sequences were only selected for study if there were five or more cycles of rhythmic chewing. Because cycle time is calculated using the relative timing of three successive strain peaks, data on strain magnitude, rate and duration from the first and last non-ingestion cycles in each chewing sequence were not analyzed, although these cycles were used to calculate cycle durations/frequencies for neighboring cycles. Most of the data sets did not allow puncture-crushing cycles, tooth-tooth contact cycles and swallowing cycles to be distinguished, so the data set includes all three. Primates are known to intercalate multiple swallows into a chewing sequence (Hylander et al., 1987; Thexton and Hiiemae, 1997), as may other species as well.

Data from all food types were pooled and analyzed together. Analyses of the data separated by food type revealed no food-related deviations from the patterns reported below.

Statistical analyses

To determine whether bite force is modulated by changes in load time and/or load rate, and whether there are resulting changes in chewing duty factor and cycle time, bivariate correlation coefficients were calculated within each experiment between strain magnitude (ϵ_1 and ϵ_2) and load time, load time STD, load rate and cycle time. To investigate relationships between strain magnitude and strain profiles in unloading, correlations between strain magnitude and unload time, and unload rate were also calculated. To determine whether bite force is modulated through changes in duty factor, correlations between strain magnitude and duty factor were also calculated. If the data did not meet the assumptions of parametric statistics (i.e. skewness and kurtosis), either when untransformed or when transformed to \log_{10} , Spearman's rho was calculated. Correlations between normally distributed and homoscedastic data combinations were estimated using Pearson's r . For each set of comparisons, significance was assessed relative to a critical value of $P=0.001$ [$0.05/(n \text{ experiments})=0.05/40=0.001$], as well as the standard, less conservative, levels of significance, $P<0.05$, $P<0.01$.

Multiple regression models were run with strain magnitude as the dependent variable and load time and strain rate as the independent variables to determine which of these variables has the greatest influence on strain magnitude. This was assessed using beta coefficients. Beta coefficients are standardized

Table 1. Sources of data used in this study

Species	Investigators	ID ⁵	Experiment ID number ⁶	Strain gage type	Gage location	Sample rate (Hz)	Foods
<i>Lama pacos</i>	Williams ¹	Perla	40	Delta rosette ¹⁰	Midcorpus	10 000	Hay
	Williams ¹	Genevieve	50	Delta rosette ¹⁰	Below M ₁ , 4–10 mm above lower border	10 000	Hay
	Williams ¹	Laura	52	Delta rosette ¹⁰	Below M ₁ , 4–10 mm above lower border	10 000	Hay
<i>Sus scrofa</i> (Hanford miniature strain)	Williams ¹	Dabreon	56	Delta rosette ¹⁰	Midcorpus	10 000	Hay
	Liu/Herring ²	Bess	101	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
	Liu/Herring ²	Freyr	102	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
	Liu/Herring ²	Lily	103	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
<i>Equus caballus</i>	Liu/Herring ²	Loci	104	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
	Liu/Herring ²	Rama	105	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
	Liu/Herring ²	Thor	106	Rectangular rosette ⁸	Below the 1st molariform tooth	500	Pig chow
	Williams ¹	Bucky	35	Delta rosette ¹⁰	Below M ₂ , 4 mm above lower border	10 000	Hay
	Williams ¹	Domino	53	Delta rosette ¹⁰	Below M ₂ , 8 mm above lower border	10 000	Hay
	Rafferty/Herring ²	2	12	Rectangular rosette ⁸		250	Hay
<i>Capra capra</i> (goat)	Rafferty/Herring ²	4	14	Rectangular rosette ⁸		250	Sweet grain
	Rafferty/Herring ²	3	16	Rectangular rosette ⁸		250	Pig chow
	Williams ¹	Domingo	20	Delta rosette ¹⁰	Below M ₂ , midcorpus	10 000	Hay
<i>Macaca fascicularis</i> (long tailed macaque)	Williams ¹	Don Quijote	33	Delta rosette ¹⁰	Below M ₃ or M ₂ , 7–12 mm above lower border	10 000	Hay
	Hylander ³	Alex (1)	79	Rectangular rosette ⁹	Lower border, M ₁	500	Apple
	Hylander ³	Mr Big (4)	791	Rectangular rosette ⁹	Lower border, M _{1,2}	500	Apple
	Hylander ³	Alex (1)	81	Delta rosette ¹⁰		500	Apple
<i>Macaca mulatta</i> (Rhesus macaque)	Hylander ³	Dole (2)	83	Delta rosette ¹⁰		500	Apple, monkey chow
	Hylander ³	Nightlady (3)	84	Delta rosette ¹⁰		500	Apple, monkey chow
	Ross ⁴	Edith	38	Delta rosette ¹⁰	Lower border, P ₄	2700	Almond, apricot, prune
	Ross ⁴	Laverne	46	Delta rosette ¹⁰	Lower border, M ₁	2700	Apple, jawbreaker, taffy
	Ross ⁴	Shirley	48	Delta rosette ¹⁰	5 mm from lower border, M ₁	2700	Apple, grape

Table continued on next page

Table 1. Continued

Species	Investigators	ID ⁵	Experiment ID number ⁶	Strain gage type	Gage location	Sample rate (Hz)	Foods
<i>Chlorocebus aethiops</i> (vervet monkey)	Ross ⁴	Male	59	Delta rosette ¹⁰	Mid corpus, P ₄	1000	Apple, grape, prune
	Ross ⁴	Male	96	Delta rosette ¹⁰	Lower border, M ₁	10 000	Apple corn, pineapple, prune
<i>Aotus trivirgatus</i> (owl monkey)	Ross/Hylander ³	1	9	Delta rosette ¹⁰	5 mm from lower border, M ₁	10 000	Apple, apricot, carrot, gummy bear, plantains, prune
	Ross/Hylander ³	2	10	Delta rosette ¹⁰	Mid corpus, M ₁	10 000	Apple, gummy bear, prune
	Ross ⁴	3	31	Delta rosette ¹⁰	Lower border, M ₂	2700	Apple, gummy bear, prune
<i>Otolemur crassicaudatus</i> (greater bushbaby)	Ravosa/Hylander ³	Elfu	921	Delta rosette ¹⁰	Lower border, M ₁₋₂	500	Gummy bear
	Ravosa/Hylander ³	Marjoni	922	Delta rosette ¹⁰	Mid corpus, M ₁	500	Prune
	Ross ⁴	SB female	28	Delta rosette ¹⁰	? M ₃	600	Gummy bear
	Ross ⁴	V and females	63	Delta rosette ¹⁰	Lower border, M ₂	2700	Gummy bear, raisin
<i>Eulemur fulvus rufus</i> (brown lemur)	Ross ⁴	Bao	67	Delta rosette ¹⁰	Mid corpus, M ₂	1000	Apple, grape, raisin
	Ross ⁴	Beby	70	Delta rosette ¹⁰	Two gages: Mid corpus, M ₂ , Mid corpus, P ₄	1000	Apple, grape, prune, raisin
	Ross ⁴	Haja	71	Delta rosette ¹⁰	Mid corpus, M ₁	1000	Apple, grape, raisin
<i>Varecia variegata rubra</i> (red ruffed lemur)	Ross ⁴	Borealis	91	Delta rosette ¹⁰	Mid corpus, M ₁	1000	Pineapple, raisin
	Ross ⁴	Diphda	93	Delta rosette ¹⁰	Lower border, M ₁	1000	Apple, raisin
	Ross ⁴	Borealis	94	Delta rosette ¹⁰	Lower border, M ₁	1000	Strawberry, prune, raisin

M₁, 1st lower molar; M₂, 2nd lower molar; M₃, 3rd lower molar; P₄, 4th lower premolar.¹Duke University, Research Farm of the Department of Lab Animal Resources located in Durham, NC, USA.²University of Washington.³Duke University, Biological Anthropology and Anatomy.⁴Stony Brook University.⁵ID is animal ID given by experimenter who collected data.⁶Experiment ID is ID number in Ross data files.⁷N11-FA-2-120-11, Showa.⁸SK-06-030WR-120, Micro-Measurements, Raleigh, NC, USA.⁹WA-06-030WR-120, Micro-Measurements.¹⁰SA-06-030WY-120, Micro-Measurements.

regression coefficients obtained when all variables are standardized by conversion to z -scores. Beta coefficients express the relative standardized strengths of the effects of the independent variables on strain magnitude. The multiple regression models were run on z -scores using the General Linear Model univariate procedure in SPSS 12.0 in order to test for interaction effects. These were not significant, so the data were run again using the Multiple Regression procedure in order to simultaneously estimate the best model without interaction effects, as well as to obtain diagnostics of multicollinearity. Multicollinearity between independent variables in a multiple regression equation (in this case, load rate and load time) has significant effects on estimates of their partial slope coefficients. Specifically, the correlation between the estimators of the partial slope coefficients is the inverse of the correlation between the independent variables (Berry and Feldman, 1985); consequently, a high degree of multicollinearity weakens conclusions regarding the relative impacts of the two independent variables on the dependent variable. To assess the degree of multicollinearity, the correlation coefficients between strain rate and load time are also presented, along with the 'tolerance' statistic calculated by SPSS. The tolerance for a variable is the proportion of the variance in that variable not accounted for by other independent variables in the model. A low value indicates that the variable contributes little to the model independent of the other variables, and is an indicator of multicollinearity between independent variables.

Various multiple regression iterations were run in order to find the model that best explains the variance in strain magnitude with all variables significant. Only data that met the assumptions of linear regression were analyzed.

Results

Bivariate correlations

The bivariate correlations between ϵ_1 magnitude and load rate, load time, load time STD, cycle time, duty factor, unload rate and unload time are given in Table 2; the bivariate correlations between ϵ_2 magnitude and load rate, load time, load time STD, cycle time, duty factor, unload rate and unload time are given in Table 3. The results of the analyses using raw and logged data are very similar, and only the results using raw data are presented here. Fig. 3, Fig. 4, Fig. 5, Fig. 6 illustrate the relationships between ϵ_1 magnitudes and both load rate and load time in four experiments: Experiment 71 on *Eulemur*, Experiment 9 on *Aotus*, Experiment 103 on *Sus*, and Experiment 16 on *Capra*.

Strain magnitude is significantly correlated with strain rate in the majority of experiments. ϵ_1 magnitude is significantly ($P \leq 0.001$) correlated with ϵ_1 load rate in 32 out of 40 experiments, and ϵ_2 magnitude is significantly ($P \leq 0.001$) correlated with ϵ_2 load rate in 31 out of 40 experiments. In contrast, ϵ_1 magnitude is only significantly ($P \leq 0.001$) correlated with ϵ_1 load time, load time STD and cycle time in 9, 17, and 3 out of 40 experiments, respectively; and ϵ_2

magnitude is only significantly ($P \leq 0.001$) correlated with ϵ_2 load time, load time STD, and cycle time in 8, 6, and 4 out of 40 experiments, respectively. ϵ_1 magnitude was significantly ($P \leq 0.001$) correlated with duty factor in 6 out of 40 experiments and ϵ_2 magnitude was significantly ($P \leq 0.001$) correlated with duty factor in 9 out of 40 experiments.

Strain magnitude is significantly correlated with unload rate in the majority of experiments (ϵ_1 magnitude, 34/40 experiments; ϵ_2 magnitude, 32/40 experiments). ϵ_1 magnitude was significantly ($P \leq 0.001$) correlated with unload time in only 9 out of 40 experiments, and ϵ_2 magnitude was

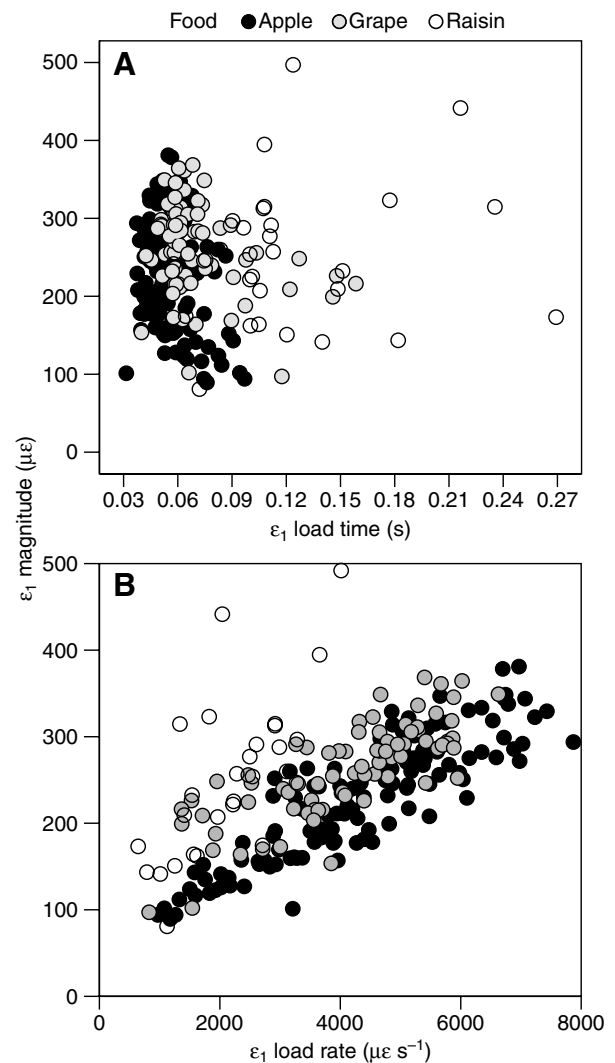


Fig. 3. Bivariate plots of ϵ_1 magnitude in microstrain ($\mu\epsilon$) against loading time (in s) (A) and loading rate in $\mu\epsilon \text{ s}^{-1}$ (B). Data recorded during Experiment 71 on *Eulemur fulvus* eating apple (black circles), grapes (grey circles) and raisins (open circles). Note that there is not a significant correlation between strain magnitude and loading time (A), but there is a significant correlation between strain magnitude and loading rate (B). Although these data are not presented here, it is clear that these patterns of relationship (or lack thereof) also apply within different food types, although the nature of the relationship (i.e. the slope) may vary across food types.

Table 2. Correlation coefficients for ϵ_i data

Species	Experiment	Magnitude vs rate	Magnitude vs load time	Magnitude vs cycle time	Magnitude vs load time STD	Rate vs load time	Magnitude vs load time STD	Magnitude vs cycle time	Magnitude vs duty factor	Magnitude vs unload time	Magnitude vs unload rate	Unload rate vs unload time
<i>Aotus</i>	9	0.584*** (243)	0.263*** (243)	-0.570*** (243)	0.168** (243)	0.299*** (384)	0.383*** (167)	0.527*** (155)	0.770*** (155)	-0.056 ^{NS} (155)		
<i>Aotus</i>	10	0.767*** (181)	-0.248*** (181)	-0.790*** (181)	-0.314*** (181)	0.089 ^{NS} (195)	-0.117 ^{NS} (167)	0.432*** (169)	0.600*** (169)	-0.380*** (169)		
<i>Aotus</i>	31	0.596*** (113)	0.520*** (113)	-0.260*** (113)	0.027 ^{NS} (113)	0.232* (119)	-0.051 ^{NS} (103)	0.284*** (97)	0.470*** (97)	-0.618*** (97)		
<i>Capra</i>	12	0.668*** (24)	-0.023 ^{NS} (24)	-0.698*** (24)	-0.003 ^{NS} (24)	-0.244 ^{NS} (24)	-0.017 ^{NS} (20)	-0.354 ^{NS} (23)	0.658*** (23)	-0.917*** (23)		
<i>Capra</i>	14	0.897*** (24)	-0.481* (24)	-0.696*** (24)	-0.420* (24)	0.073 ^{NS} (28)	-0.633*** (28)	-0.088 ^{NS} (21)	0.924*** (21)	-0.452* (21)		
<i>Capra</i>	16	0.906*** (22)	-0.368 ^{NS} (22)	-0.681*** (22)	-0.542*** (22)	0.540*** (22)	-0.684*** (16)	0.434*** (22)	0.706*** (22)	-0.076 ^{NS} (22)		
<i>Capra</i>	20	0.745*** (47)	0.232 ^{NS} (47)	-0.434*** (47)	0.274 ^{NS} (43)	-0.058 ^{NS} (44)	0.408*** (44)	0.320*** (47)	0.768*** (47)	-0.321* (47)		
<i>Capra</i>	33	0.375* (45)	0.582*** (45)	-0.414*** (45)	0.554*** (41)	-0.349* (41)	-0.029 ^{NS} (26)	0.280 ^{NS} (45)	0.596*** (45)	-0.591*** (45)		
<i>Chlorocebus</i>	59	0.345* (35)	0.379* (35)	-0.700*** (35)	0.454*** (35)	0.081 ^{NS} (63)	0.204 ^{NS} (14)	-0.065 ^{NS} (18)	0.660*** (18)	-0.517* (18)		
<i>Chlorocebus</i>	96	0.571*** (86)	0.036 ^{NS} (86)	-0.735*** (86)	-0.084 ^{NS} (86)	0.108 ^{NS} (87)	0.109 ^{NS} (75)	0.530*** (86)	0.675*** (86)	-0.183 ^{NS} (86)		
<i>Equus</i>	35	0.906*** (38)	-0.548*** (38)	-0.841*** (38)	-0.413* (34)	0.164 ^{NS} (36)	0.008 ^{NS} (33)	0.360* (39)	0.630*** (39)	-0.469*** (39)		
<i>Equus</i>	53	0.548*** (54)	-0.080 ^{NS} (54)	-0.874*** (54)	0.262 ^{NS} (52)	-0.380*** (54)	0.213 ^{NS} (51)	0.233 ^{NS} (53)	0.113 ^{NS} (53)	-0.916*** (53)		
<i>Eulemur</i>	67	0.784*** (81)	0.181 ^{NS} (81)	-0.456*** (81)	0.186 ^{NS} (81)	-0.322*** (93)	0.270* (60)	-0.384*** (92)	0.918*** (92)	-0.691*** (92)		
<i>Eulemur</i>	70	0.472*** (75)	0.205 ^{NS} (75)	-0.737*** (75)	-0.036 ^{NS} (75)	0.251* (83)	-0.251* (75)	0.284* (73)	0.743*** (73)	-0.411*** (73)		
<i>Eulemur</i>	71	0.701*** (233)	-0.080 ^{NS} (233)	-0.719*** (233)	-0.115 ^{NS} (233)	0.061 ^{NS} (235)	-0.138* (230)	-0.128 ^{NS} (220)	0.783*** (220)	-0.643*** (220)		
<i>Lama</i>	40	0.522*** (27)	0.071 ^{NS} (27)	-0.761*** (27)	-0.281 ^{NS} (25)	0.328 ^{NS} (25)	-0.235 ^{NS} (25)	0.173 ^{NS} (27)	0.367 ^{NS} (27)	-0.839*** (27)		
<i>Lama</i>	50	0.917*** (65)	-0.500*** (65)	-0.740*** (65)	-0.462*** (58)	-0.148 ^{NS} (62)	0.452*** (49)	0.196 ^{NS} (64)	0.937*** (64)	-0.116 ^{NS} (64)		
<i>Lama</i>	52	0.534*** (32)	0.386* (32)	-0.492*** (32)	0.271 ^{NS} (30)	0.245 ^{NS} (30)	0.102 ^{NS} (29)	0.047 ^{NS} (31)	0.581*** (31)	-0.666*** (31)		
<i>Lama</i>	56	0.795*** (17)	-0.012 ^{NS} (17)	-0.598* (17)	-0.259 ^{NS} (15)	0.423 ^{NS} (15)	0.211 ^{NS} (16)	0.211 ^{NS} (16)	0.859*** (16)	-0.309 ^{NS} (16)		
<i>Macaca</i>	38	-0.096 ^{NS} (152)	0.576*** (152)	-0.832*** (152)	0.643*** (152)	-0.292*** (167)	0.427*** (158)	0.261*** (159)	0.301*** (159)	-0.801*** (159)		
<i>Macaca</i>	46	0.519*** (59)	0.108 ^{NS} (59)	-0.745*** (59)	0.373*** (59)	-0.104 ^{NS} (62)	0.471*** (54)	0.029 ^{NS} (56)	0.741*** (56)	-0.577*** (56)		
<i>Macaca</i>	48	0.296*** (80)	0.366*** (80)	-0.738*** (80)	0.269* (80)	0.213* (95)	-0.006 ^{NS} (85)	0.479*** (76)	0.219 ^{NS} (76)	-0.702*** (76)		
<i>Macaca</i>	79	0.626*** (55)	-0.283* (55)	-0.901*** (55)	-0.018 ^{NS} (55)	-0.472*** (55)	0.301* (53)	0.111 ^{NS} (48)	0.329* (48)	-0.881*** (48)		
<i>Macaca</i>	81	0.658*** (46)	0.007 ^{NS} (46)	-0.694*** (46)	-0.135 ^{NS} (46)	-0.086 ^{NS} (66)	0.180 ^{NS} (63)	0.026 ^{NS} (17)	0.565* (17)	-0.748*** (17)		
<i>Macaca</i>	83	0.705*** (94)	-0.006 ^{NS} (94)	-0.649*** (94)	-0.150 ^{NS} (94)	0.032 ^{NS} (101)	0.543*** (99)	-0.119 ^{NS} (95)	0.744*** (95)	-0.675*** (95)		
<i>Macaca</i>	84	0.722*** (46)	0.163 ^{NS} (46)	-0.497*** (46)	0.033 ^{NS} (46)	0.084 ^{NS} (52)	0.434*** (51)	0.628*** (42)	0.544*** (42)	-0.292 ^{NS} (42)		
<i>Macaca</i>	791	0.440* (22)	0.489* (22)	-0.461* (22)	0.582*** (22)	-0.301 ^{NS} (40)	0.444*** (40)					
<i>Ootemur</i>	28	0.830*** (21)	0.386 ^{NS} (21)	-0.191 ^{NS} (21)	0.399 ^{NS} (21)	-0.096 ^{NS} (21)	0.284 ^{NS} (21)	0.484* (21)	0.924*** (21)	0.119 ^{NS} (21)		
<i>Ootemur</i>	63	0.916*** (26)	0.411* (26)	0.173 ^{NS} (26)	0.301 ^{NS} (26)	-0.114 ^{NS} (26)	0.607*** (26)	0.324 ^{NS} (24)	0.874*** (24)	-0.138 ^{NS} (24)		
<i>Ootemur</i>	921	0.820*** (89)	-0.082 ^{NS} (89)	-0.605*** (89)	-0.221* (89)	0.280*** (91)	-0.150 ^{NS} (90)	-0.224* (87)	0.818*** (87)	-0.740*** (87)		
<i>Ootemur</i>	922	0.802*** (13)	0.690*** (13)	0.158 ^{NS} (13)	0.473 ^{NS} (13)	0.515 ^{NS} (13)	0.130 ^{NS} (13)	-0.383 ^{NS} (9)	0.978*** (9)	-0.567 ^{NS} (9)		
<i>Sus</i>	101	0.917*** (27)	0.571*** (27)	0.271 ^{NS} (27)	0.535*** (27)	-0.035 ^{NS} (50)	-0.103 ^{NS} (28)	0.658*** (34)	0.873*** (34)	0.285 ^{NS} (34)		
<i>Sus</i>	102	0.891*** (45)	0.764*** (45)	0.355* (45)	0.681*** (45)	-0.179 ^{NS} (45)	0.402*** (45)	0.388*** (45)	0.938*** (45)	0.134 ^{NS} (45)		
<i>Sus</i>	103	0.890*** (49)	-0.104 ^{NS} (49)	-0.533*** (49)	-0.275 ^{NS} (49)	0.347*** (66)	-0.703*** (53)	0.656*** (33)	0.618*** (33)	0.033 ^{NS} (33)		
<i>Sus</i>	104	0.827*** (178)	0.027 ^{NS} (178)	-0.489*** (178)	0.053 ^{NS} (178)	0.082 ^{NS} (198)	-0.111 ^{NS} (174)	0.122 ^{NS} (187)	0.849*** (187)	-0.363*** (187)		
<i>Sus</i>	105	0.357* (38)	-0.163 ^{NS} (38)	-0.907*** (38)	-0.138 ^{NS} (38)	-0.020 ^{NS} (49)	0.186 ^{NS} (21)	0.309* (49)	0.926*** (49)	-0.070 ^{NS} (49)		
<i>Sus</i>	106	0.118 ^{NS} (16)	0.165 ^{NS} (16)	-0.926*** (16)	0.203 ^{NS} (16)	0.053 ^{NS} (47)	-0.237 ^{NS} (41)	-0.028 ^{NS} (36)	0.640*** (36)	-0.721*** (36)		
<i>Varecia</i>	91	0.861*** (51)	-0.230 ^{NS} (51)	-0.667*** (51)	-0.370*** (51)	0.320* (51)	-0.413*** (46)	0.248 ^{NS} (48)	0.888*** (48)	-0.188 ^{NS} (48)		
<i>Varecia</i>	93	0.903*** (44)	-0.040 ^{NS} (44)	-0.438*** (44)	-0.272 ^{NS} (44)	0.195 ^{NS} (51)	-0.072 ^{NS} (27)	-0.009 ^{NS} (28)	0.866*** (28)	-0.410* (28)		
<i>Varecia</i>	94	0.859*** (52)	-0.302* (52)	-0.658*** (52)	-0.270 ^{NS} (52)	-0.161 ^{NS} (53)	-0.016 ^{NS} (41)	-0.189 ^{NS} (48)	0.943*** (48)	-0.481*** (48)		

Values are correlation coefficients (Pearson's r , or Spearman's rho); sample size is given in parentheses. NS, not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Sample sizes vary within an experiment because not all variables could be measured in all cycles.

Table 3. Correlation coefficients for ϵ_2 data

Species	Experiment	Magnitude vs rate	Magnitude vs load time	Rate vs load time	Magnitude vs load time STD	Magnitude vs cycle time	Magnitude vs duty factor	Magnitude vs unload time	Magnitude vs unload rate	Unload rate vs unload time
<i>Aotus</i>	9	0.734*** (251)	-0.399*** (251)	0.241*** (251)	-0.214*** (251)	-0.321*** (384)	-0.402*** (167)	-0.523*** (195)	0.802*** (195)	0.017 ^{NS} (195)
<i>Aotus</i>	10	0.612*** (181)	0.058 ^{NS} (181)	0.797*** (181)	0.013 ^{NS} (181)	0.099 ^{NS} (195)	-0.235*** (167)	-0.458*** (176)	0.524*** (176)	0.425*** (176)
<i>Aotus</i>	31	0.709*** (112)	-0.237* (112)	0.394*** (112)	-0.049 ^{NS} (112)	-0.108 ^{NS} (119)	0.088 ^{NS} (103)	0.021 ^{NS} (109)	0.825*** (109)	0.535*** (109)
<i>Capra</i>	12	0.750*** (20)	0.556* (20)	0.928*** (20)	0.553* (20)	0.150 ^{NS} (24)	0.405 ^{NS} (20)	-0.306 ^{NS} (24)	0.296 ^{NS} (24)	0.793*** (24)
<i>Capra</i>	14	0.900*** (28)	0.648*** (28)	0.894*** (28)	0.666*** (28)	-0.141 ^{NS} (28)	0.624*** (28)	0.061 ^{NS} (28)	0.846*** (28)	0.556*** (28)
<i>Capra</i>	16	0.826*** (16)	0.422 ^{NS} (16)	0.844*** (16)	0.509* (16)	-0.516* (22)	0.590* (16)	-0.307 ^{NS} (22)	0.942*** (22)	0.023 ^{NS} (22)
<i>Capra</i>	20	0.901*** (48)	0.247 ^{NS} (48)	0.555*** (48)	0.128 ^{NS} (44)	0.038 ^{NS} (44)	-0.165 ^{NS} (44)	-0.615*** (48)	0.817*** (48)	-0.080 ^{NS} (48)
<i>Capra</i>	33	0.461* (28)	-0.168 ^{NS} (28)	0.778*** (28)	-0.139 ^{NS} (28)	0.078 ^{NS} (41)	-0.266 ^{NS} (26)	-0.250 ^{NS} (26)	0.549*** (26)	0.652*** (26)
<i>Chlorocebus</i>	59	0.076 ^{NS} (25)	-0.295 ^{NS} (25)	0.827*** (25)	-0.233 ^{NS} (25)	-0.134 ^{NS} (63)	-0.385 ^{NS} (14)	-0.449*** (34)	0.526*** (34)	0.428* (34)
<i>Chlorocebus</i>	96	0.350*** (79)	-0.257* (79)	0.760*** (79)	-0.094 ^{NS} (79)	-0.138 ^{NS} (87)	-0.191 ^{NS} (75)	-0.405*** (82)	0.512*** (82)	0.486*** (82)
<i>Equus</i>	35	0.904*** (39)	0.072 ^{NS} (39)	0.630*** (39)	0.185 ^{NS} (35)	-0.198 ^{NS} (36)	-0.030 ^{NS} (33)	-0.575*** (38)	0.821*** (38)	-0.181 ^{NS} (38)
<i>Equus</i>	53	-0.104 ^{NS} (55)	-0.459*** (55)	0.956*** (55)	-0.516*** (51)	0.437*** (54)	-0.524*** (51)	-0.006 ^{NS} (58)	0.481*** (58)	0.860*** (58)
<i>Eulemur</i>	67	0.811*** (60)	0.233 ^{NS} (60)	0.688*** (60)	0.164 ^{NS} (60)	0.282*** (93)	-0.016 ^{NS} (60)	-0.313*** (93)	0.659*** (93)	0.414*** (93)
<i>Eulemur</i>	70	0.826*** (75)	0.404*** (75)	0.814*** (75)	0.274* (75)	-0.034 ^{NS} (83)	0.118 ^{NS} (75)	-0.156 ^{NS} (80)	0.760*** (80)	0.472*** (80)
<i>Eulemur</i>	71	0.813*** (232)	0.091 ^{NS} (232)	0.602*** (232)	0.121 ^{NS} (232)	0.016 ^{NS} (235)	0.230*** (230)	0.281*** (231)	0.914*** (231)	0.603*** (231)
<i>Lama</i>	40	0.303 ^{NS} (27)	-0.087 ^{NS} (27)	0.849*** (27)	0.025 ^{NS} (25)	-0.391 ^{NS} (25)	0.248 ^{NS} (25)	0.275 ^{NS} (26)	0.482* (26)	0.943*** (26)
<i>Lama</i>	50	0.696*** (58)	-0.213 ^{NS} (58)	0.489*** (58)	-0.229 ^{NS} (51)	0.204 ^{NS} (62)	-0.537*** (49)	-0.399*** (58)	0.714*** (58)	0.384*** (58)
<i>Lama</i>	52	0.515*** (32)	-0.393* (32)	0.560*** (32)	-0.287 ^{NS} (30)	-0.157 ^{NS} (30)	-0.159 ^{NS} (29)	0.109 ^{NS} (31)	0.537*** (31)	0.846*** (31)
<i>Lama</i>	56	0.894 ^{NS} (4)	0.800 ^{NS} (4)	0.984* (4)	-0.486 ^{NS} (15)	-0.486 ^{NS} (15)	-0.536 ^{NS} (7)	-0.571 ^{NS} (7)	0.964*** (7)	0.964*** (7)
<i>Macaca</i>	38	-0.190* (162)	-0.541*** (162)	0.906*** (162)	-0.549*** (162)	0.236** (167)	-0.472*** (158)	-0.059 ^{NS} (162)	0.310*** (162)	0.908*** (162)
<i>Macaca</i>	46	0.466*** (58)	0.031 ^{NS} (58)	0.864*** (58)	-0.273* (58)	0.002 ^{NS} (62)	-0.231 ^{NS} (54)	-0.070 ^{NS} (54)	0.602*** (54)	0.703*** (54)
<i>Macaca</i>	48	0.665*** (90)	0.100 ^{NS} (90)	0.789*** (90)	0.079 ^{NS} (90)	-0.007 ^{NS} (95)	-0.013 ^{NS} (85)	-0.290*** (86)	0.503*** (86)	0.702*** (86)
<i>Macaca</i>	79	0.541*** (55)	0.033 ^{NS} (55)	0.810*** (55)	-0.157 ^{NS} (55)	0.450*** (55)	-0.281* (53)	-0.189 ^{NS} (53)	0.408*** (53)	0.773*** (53)
<i>Macaca</i>	81	0.660*** (65)	0.033 ^{NS} (65)	0.735*** (65)	0.006 ^{NS} (65)	0.099 ^{NS} (66)	-0.119 ^{NS} (63)	-0.076 ^{NS} (64)	0.522*** (64)	0.757*** (64)
<i>Macaca</i>	83	0.702*** (100)	-0.551*** (100)	0.024 ^{NS} (100)	-0.423*** (100)	-0.002 ^{NS} (101)	-0.572*** (99)	-0.628*** (100)	0.565*** (100)	0.071 ^{NS} (100)
<i>Macaca</i>	84	0.760*** (52)	-0.146 ^{NS} (52)	0.446*** (52)	-0.069 ^{NS} (52)	-0.165 ^{NS} (52)	-0.449*** (51)	-0.594*** (51)	0.294* (51)	0.510*** (51)
<i>Macaca</i>	791	0.653*** (40)	-0.130 ^{NS} (40)	0.580*** (40)	-0.295 ^{NS} (40)	0.225 ^{NS} (40)	-0.248 ^{NS} (40)	0.220 ^{NS} (40)	0.732*** (40)	0.788*** (40)
<i>Otolemur</i>	28	0.775*** (21)	-0.321 ^{NS} (21)	0.345 ^{NS} (21)	-0.087 ^{NS} (21)	-0.128 ^{NS} (21)	-0.097 ^{NS} (21)	-0.821*** (21)	0.865*** (21)	-0.486* (21)
<i>Otolemur</i>	63	0.911*** (26)	-0.562*** (26)	-0.193 ^{NS} (26)	-0.467* (26)	0.072 ^{NS} (26)	-0.599*** (26)	-0.557*** (26)	0.863*** (26)	-0.083 ^{NS} (26)
<i>Otolemur</i>	921	0.834*** (90)	-0.175 ^{NS} (90)	0.403*** (90)	0.005 ^{NS} (90)	-0.266* (91)	0.087 ^{NS} (90)	-0.085 ^{NS} (91)	0.970*** (91)	0.108 ^{NS} (91)
<i>Otolemur</i>	922	0.897*** (13)	-0.750*** (13)	-0.410 ^{NS} (13)	-0.513 ^{NS} (13)	-0.474 ^{NS} (13)	-0.223 ^{NS} (13)	-0.008 ^{NS} (13)	0.969*** (13)	0.225 ^{NS} (13)
<i>Sus</i>	101	0.826*** (48)	0.069 ^{NS} (48)	0.566*** (48)	-0.091 ^{NS} (48)	0.320* (50)	-0.177 ^{NS} (28)	0.083 ^{NS} (29)	0.884*** (29)	0.441* (29)
<i>Sus</i>	102	0.920*** (45)	-0.538*** (45)	-0.250 ^{NS} (45)	-0.339* (45)	0.138 ^{NS} (45)	-0.369* (45)	-0.539*** (45)	0.965*** (45)	-0.364* (45)
<i>Sus</i>	103	0.912*** (65)	0.440*** (65)	0.722*** (65)	0.565*** (65)	-0.654*** (66)	0.681*** (53)	0.576*** (53)	0.903*** (53)	0.820*** (53)
<i>Sus</i>	104	0.900*** (181)	0.084 ^{NS} (181)	0.453*** (181)	0.115 ^{NS} (181)	-0.189*** (198)	-0.099 ^{NS} (174)	-0.383*** (186)	0.799*** (186)	0.179* (186)
<i>Sus</i>	105	-0.208 ^{NS} (22)	-0.391 ^{NS} (22)	0.946*** (22)	-0.461* (22)	0.230 ^{NS} (49)	-0.601** (21)	-0.320 ^{NS} (31)	0.912*** (31)	0.093 ^{NS} (31)
<i>Sus</i>	106	0.899*** (42)	0.255 ^{NS} (42)	0.528*** (42)	-0.022 ^{NS} (42)	0.086 ^{NS} (47)	-0.002 ^{NS} (41)	0.048 ^{NS} (46)	0.539*** (46)	0.820*** (46)
<i>Varecia</i>	91	0.857*** (47)	0.128 ^{NS} (47)	0.586*** (47)	0.226 ^{NS} (47)	-0.252 ^{NS} (51)	0.371* (46)	-0.114 ^{NS} (48)	0.941*** (48)	0.239 ^{NS} (48)
<i>Varecia</i>	93	0.779*** (46)	0.153 ^{NS} (46)	0.265 ^{NS} (46)	0.254 ^{NS} (46)	-0.177 ^{NS} (51)	0.115 ^{NS} (27)	-0.367* (29)	0.666*** (29)	0.142 ^{NS} (29)
<i>Varecia</i>	94	0.892*** (45)	0.444*** (45)	0.784*** (45)	0.269 ^{NS} (45)	0.209 ^{NS} (53)	0.092 ^{NS} (41)	-0.241 ^{NS} (47)	0.951*** (47)	0.101 ^{NS} (47)

Values are correlation coefficients (Pearson's r , or Spearman's ρ); sample size is given in parentheses. NS, not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Sample sizes vary within an experiment because not all variables could be measured in all cycles.

significantly ($P \leq 0.001$) correlated with unload time in 12 out of 40 experiments.

In the majority of experiments the highest correlation coefficients were observed between strain magnitude and load rate. Out of those experiments in which ϵ_1 magnitude was significantly correlated with both load time and load rate, ϵ_1 magnitude was only most highly correlated with load time in three experiments, one on goats and two on macaques. ϵ_2 magnitude was not more highly correlated with load time than load rate in any experiment in which the correlation was significant.

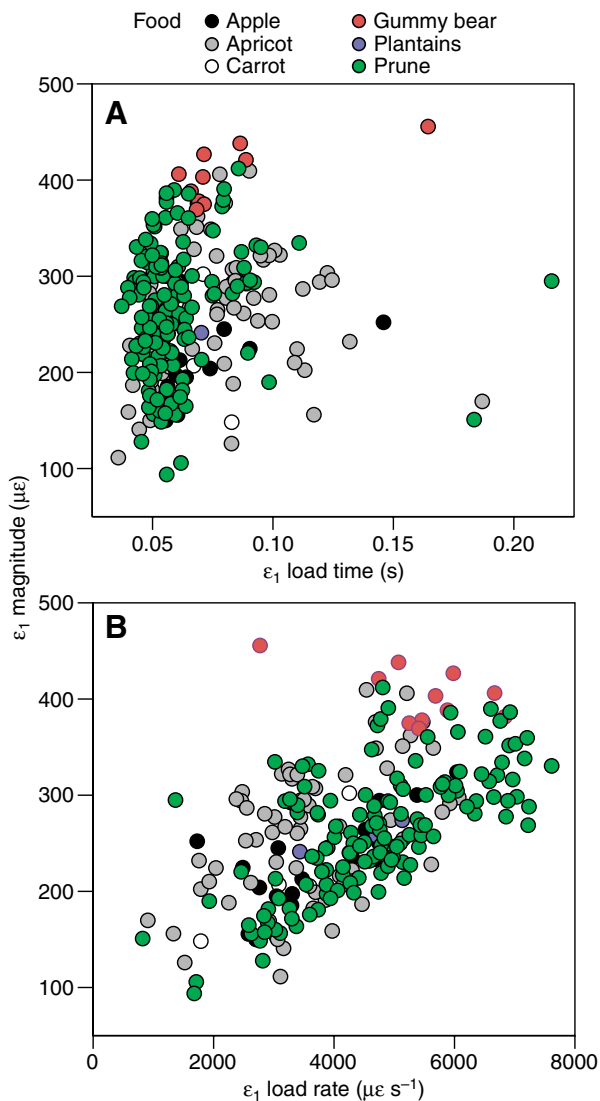


Fig. 4. Bivariate plots of ϵ_1 magnitude in microstrain ($\mu\epsilon$) against loading time (in s) (A) and loading rate in $\mu\epsilon \text{ s}^{-1}$ (B). Data recorded during Experiment 9 on *Aotus* eating a range of foods. Note that there is not a significant correlation between strain magnitude and loading time (A), but there is a significant correlation between strain magnitude and loading rate (B). It is of interest that these patterns of relationship (or lack thereof) apply within most, but not all, of the different food types. Variations in these relationships within food type are not consistent across experiments.

In sum, principal strain magnitudes are most often and most highly correlated with estimates of loading rate rather than loading time. Principal strain magnitudes are also most often and most highly correlated with unloading rates, rather than unloading times.

Multiple regressions

Data on strain magnitude, strain rate and load time from 11 out of 40 experiments met the assumptions of multiple regression (i.e. were homoscedastic and normally distributed). A total of 16 multiple regression equations was calculated. In three experiments, both the ϵ_1 and the ϵ_2 data could be analyzed; in four experiments, only the ϵ_1 data could be analyzed; and in

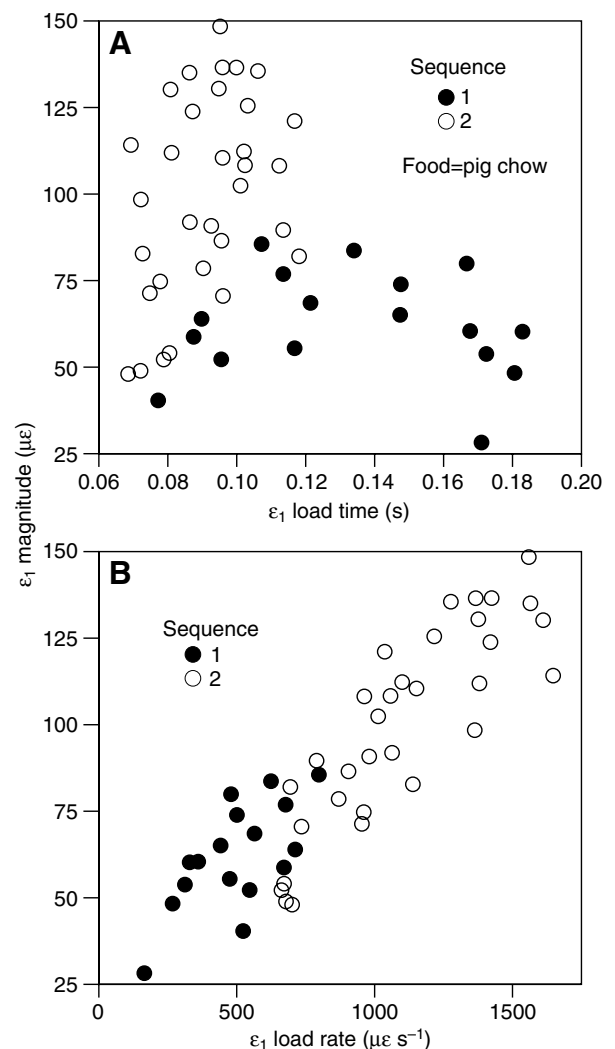


Fig. 5. Bivariate plots of ϵ_1 magnitude in microstrain ($\mu\epsilon$) against loading time (in s) (A) and loading rate in $\mu\epsilon \text{ s}^{-1}$ (B). Data recorded during Experiment 103 on *Sus* eating pig chow. The data are labeled by chewing sequence. Note that, across all chews, there is not a significant correlation between strain magnitude and loading time (A), but there is a significant correlation between strain magnitude and loading rate (B). Analyses of data within chewing sequences reveal that these patterns are also seen within sequences.

five experiments, only the ϵ_2 data could be analyzed (Table 4, Table 5).

Multiple regressions of strain magnitude against load rate and load time are highly significant, with adjusted r^2 values ranging from 0.669–0.996, all but one being >0.900 . In all 16 cases, the beta (standardized partial slope) coefficients for load rate are higher (1.1–2.6 \times higher) than those for load time. These results suggest that changes in load rate have a greater impact on strain magnitude than changes in loading time.

As expected, the magnitude of the correlation between load rate and load time is related to the 'tolerance' value. As the correlations between the independent variables (load rate and load time) increase, the tolerance values decrease, indicating effects of multicollinearity. Load rate and load time are significantly ($P<0.05$) correlated in 11 of the 16 calculations. In eight experiments, load rates decrease as load time increases

(negative correlations between ϵ_1 rate and time; positive correlations between ϵ_2 rate and time); in the other eight experiments, increases in load rate are associated with increases in load time. However, interaction effects between load rate and load time were not significant in any of the experiments, indicating that load rate and load time have independent effects on strain magnitude.

Regressions of strain magnitude against all variables together and separately (load rate, load time, load time STD, cycle time and duty factor) did not generate better models than regressions only on load rate and load time. When all variables were included, neither cycle time nor load time STD contributed significantly to the model. Similarly, when strain magnitude was regressed against load rate, load time and cycle time, only cycle time contributed significantly to the model in the case of Experiment 33 (ϵ_2) with an increase in adjusted r^2

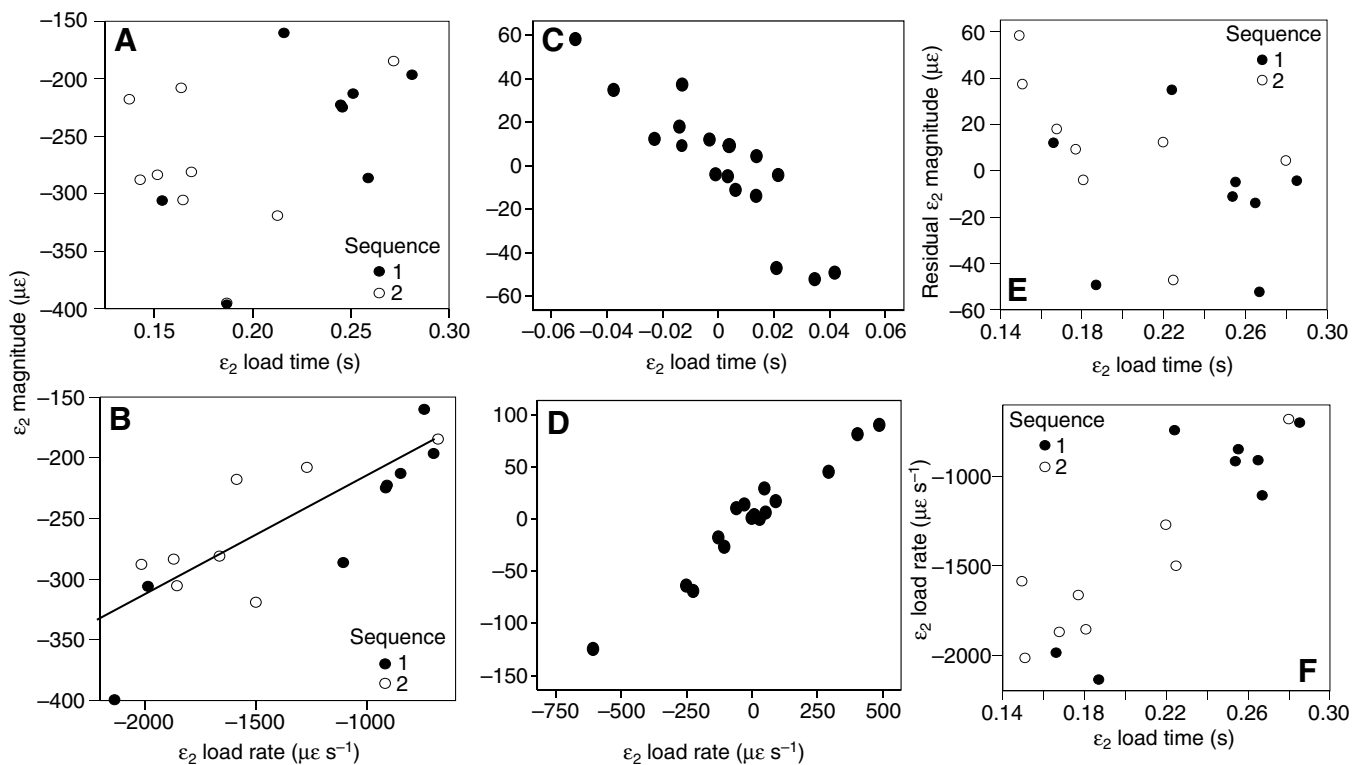


Fig. 6. Plots illustrating analysis of data from Experiment 16 on *Capra* eating hay. (A) Bivariate plot of ϵ_2 magnitude in microstrain ($\mu\epsilon$) against loading time (in s). (B) Bivariate plot of ϵ_2 magnitude in microstrain ($\mu\epsilon$) against loading rate in $\mu\epsilon \text{ s}^{-1}$. Regression equation of ϵ_2 magnitude against loading rate in $\mu\epsilon \text{ s}^{-1}$: $\epsilon_2 \text{ magnitude} = -117.07 + 0.11 \times \epsilon_2 \text{ load rate}$. (C, D) Partial regression plots from multiple regression of ϵ_2 magnitude in microstrain ($\mu\epsilon$) against loading time (in s) and loading rate in $\mu\epsilon \text{ s}^{-1}$. (E) Plot of residual ϵ_2 magnitude (i.e. variance not explained by the regression in B) against load time (s). (F) Bivariate plot of loading rate in $\mu\epsilon \text{ s}^{-1}$, against loading time (in s). There is not a significant correlation between strain magnitude and loading time (A), but there is a significant correlation between strain magnitude and loading rate (B). Partial regression plots illustrate relationship between dependent variable (ϵ_2 magnitude) and one independent variable, while holding the other variable constant. These partial regression plots suggest close relationships between strain magnitude and each independent variable when controlling for the other because, as quantified here, strain magnitude must be nearly completely explained by a combination of load rate and load time. (F) Increases in loading rate are accompanied by increases in loading time, reinforcing the conclusion that load time and load rate are both strategies employed to increase strain magnitude. However, examination of bivariate plots A and B reveals that load time explains little of the variance in strain magnitude. Once the effect of strain rate is accounted for, there is a weak relationship between residual strain magnitude and load time, as illustrated in E, with load time explaining much less of the variance in strain magnitude than load rate. The data from this experiment consist of two separate chewing sequences. The data from the two sequences are indicated by separate symbols, showing that the effects revealed across the whole experiment also obtain within chewing sequences.

Table 4. Results of multiple regression analyses of ϵ_1 magnitude (dependent variable) against load rate and load time (independent variables)

Experiment	Adjusted r^2	Variable	Beta	Zero-order correlations	Partial correlations	Tolerance
16	0.930	Load rate	1.222***	0.906***	0.963	0.536
		Load time	0.465***	-0.368 ^{NS}	0.804	0.536
		Load rate vs load Time		-0.681***		
20	0.932	Load rate	1.042***	0.745***	0.965	0.812
		Load time	0.684***	0.232 ^{NS}	0.924	0.812
		Load rate vs load Time		-0.434**		
28	0.996	Load rate	0.938***	0.916***	0.998	0.964
		Load time	0.565***	0.411 ^{NS}	0.994	0.964
		Load rate vs load Time		-0.173 ^{NS}		
53	0.974	Load rate	2.029***	0.548***	0.987	0.235
		Load time	1.694***	-0.080 ^{NS}	0.982	0.235
		Load rate vs load Time		-0.874***		
56	0.962	Load rate	1.227***	0.795***	0.983	0.642
		Load time	0.721***	-0.012 ^{NS}	0.954	0.642
		Load rate vs load Time		0.970***		
102	0.996	Load rate	0.687***	0.871***	0.996	0.875
		Load time	0.521***	0.764***	0.992	0.875
		Load rate vs load Time		-0.353*		
922	0.963	Load rate	0.711***	0.802***	0.976	0.975
		Load time	0.578***	0.690**	0.956	0.975
		load rate vs load Time		0.158 ^{NS}		

Multiple regression statistics are presented by Experiment (identified in the 1st column). The adjusted r^2 for the model is presented in the 2nd column, and the beta coefficients for strain magnitude against each individual variable (listed in 3rd column) are given with their significance levels (4th columns). The zero-order correlation coefficients from Table 2 are reproduced in the 5th column for ease of reference, along with their significance levels, and the partial correlation coefficients for the multiple regression model (6th column). The tolerance value is given in the last column. The tolerance for a variable is the proportion of the variance in that variable not accounted for by other independent variables in the model. A low value indicates that the variable contributes little to the model independent of the other variables, and is an indicator of multicollinearity.

NS, not significant ($P>0.05$); * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

from 0.906 to 0.948, and Experiment 20 (ϵ_1) (r^2 from 0.932 to 0.962). When strain magnitude was regressed against load rate, load time, and duty factor, only duty factor contributed significantly to the model in Experiment 20 (ϵ_1), and at $P=0.042$, and with only a slight increase in adjusted r^2 (from 0.932 to 0.959).

When cycle time and load time STD were combined with load rate and load time, cycle and load time STD only produced an increase in adjusted r^2 in four experiments, and these increases were very modest (0.921 to 0.925; 0.984 to 0.986; 0.974 to 0.980; 0.962 to 0.981). Substituting cycle time and load time STD for load time produced comparably modest increases in adjusted r^2 in Experiment 16 (ϵ_2) (0.936 to 0.938) and (ϵ_1) (0.930 to 0.933), Experiment 33 (ϵ_2) (0.906 to 0.949), and Experiment 922 (ϵ_1) (0.963 to 0.964).

Overall, a simple regression model including only load rate and load time as independent variables best explains variance in strain magnitude. Cycle time, duty factor and load time STD

do not explain significant amounts of variance over and above that accounted for by load time itself.

Fig. 6 illustrates the relationships between ϵ_2 magnitude and load time and load rate in the data from Experiment 16, as revealed by multiple regression analyses. The bivariate plots of ϵ_2 magnitude against loading time and loading rate illustrate the lack of a significant correlation between strain magnitude and loading time (Fig. 6A), and the significant correlation between strain magnitude and loading rate (Fig. 6B). The partial regression plots illustrate the relationships between the dependent variable (ϵ_2 magnitude) and each independent variable while holding the other independent variable constant. These partial regression plots (Fig. 6C,D) reveal close relationships between strain magnitude and each independent variable when controlling for the other because, as quantified here, strain magnitude must be nearly completely explained by a combination of load rate and load time. However, the greater importance of loading rate in explaining variance in mandible

Table 5. Multiple regression results ϵ_2 magnitude (dependent variable) against load rate and load time (independent variables)

Experiment	Adjusted r^2	Variable	Beta	Zero-order correlations	Partial correlations	Tolerance
12	0.669	Load rate	1.688***	0.750***	0.756	0.138
		Load time	-1.011*	0.556*	-0.376	0.138
		Load rate vs load Time		0.928***		
16	0.936	Load rate	1.631***	0.826***	0.966	0.288
		Load time	-0.954***	0.422 ^{NS}	-0.909	0.288
		Load rate vs load Time		0.844***		
28	0.994	Load rate	1.006***	0.775***	0.997	0.881
		Load time	-0.669***	-0.321 ^{NS}	-0.993	0.881
		Load rate vs load Time		0.345 ^{NS}		
33	0.906	Load rate	1.496***	0.461***	0.954	0.395
		Load time	-1.331***	-0.168 ^{NS}	-0.943	0.395
		Load rate vs load Time		0.778***		
48	0.921	Load rate	1.557***	0.665***	0.960	0.377
		Load time	-1.129***	0.060 ^{NS}	-0.693	0.377
		Load rate vs load Time		0.789***		
52	0.938	Load rate	1.071***	0.515**	0.965	0.686
		Load time	-0.993***	-0.393*	-0.960	0.686
		Load rate vs load Time		0.560***		
63	0.984	Load rate	0.834***	0.911***	0.911	0.963
		Load time	-0.401***	-0.562**	-0.562	0.963
		Load rate vs load Time		-0.193 ^{NS}		
922		Load rate	0.709***	0.899***	0.897	0.832
		Load time	-0.459***	0.750**	-0.750	0.832
		Load rate vs load Time		-0.410 ^{NS}		

Multiple regression statistics are presented by Experiment (identified in the 1st column). The adjusted r^2 for the model is presented in the 2nd column, and the beta coefficients for strain magnitude against each individual variable (listed in 3rd column) are given with their significance levels (4th columns). The zero-order correlation coefficients from Table 2 are reproduced in the 5th column for ease of reference, along with their significance levels, and the partial correlation coefficients for the multiple regression model (6th column). The tolerance value is given in the last column. The tolerance for a variable is the proportion of the variance in that variable not accounted for by other independent variables in the model. A low value indicates that the variable contributes little to the model independent of the other variables, and is an indicator of multicollinearity.

NS, not significant ($P>0.05$); * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

strain magnitude is illustrated by Fig. 6E, a bivariate plot of the residual ϵ_2 magnitude from Fig. 6B (i.e. the variance in ϵ_2 magnitude not explained by the regression in B) against loading time. Once the effect of strain rate is accounted for, there is only a very weak relationship between residual strain magnitude and load time, as illustrated in Fig. 6E, with load time explaining much less of the variance in strain magnitude than load rate. Fig. 6F illustrates that increases in loading rate are also accompanied by increases in loading time, suggesting that increases in load magnitudes are accompanied by both increases in load rate and load time.

Discussion

This study uses mandibular corpus bone strain data to make inferences about how mammals modulate their bite forces during mastication. Two competing hypotheses were evaluated: that bite force is modulated primarily by modulating loading times, with consequent changes in chew cycle time and/or duty factor; or that bite force is modulated primarily by

modulating loading rates. Across all nine genera of mammals examined here, strain magnitude is predominantly correlated with strain load rate, and less often with cycle or loading time. In addition, strain magnitude is usually more highly correlated with strain loading rate than with loading time or cycle time. Multiple regression results confirm that changes in strain loading rate have a greater influence on strain magnitude than do changes in loading time, but they also suggest that when changes in strain loading rate are taken into account, changes in strain magnitude are consistently associated with increases in loading time. These results suggest that during rhythmic mastication in mammals, mandibular bone strain magnitude and, by inference, bite force, are increased primarily by increasing the rate at which the mandible is loaded and, to a lesser extent, by increases in the duration of loading.

Time-modulation of bite force

The results presented here stand in apparent contrast to reports by various workers that cycle duration increases with increasing hardness of foods during chewing, or of materials

placed between the teeth during cortically evoked rhythmic jaw movements (CRJMs) (Hidaka et al., 1997; Lavigne et al., 1987; Liu et al., 1998; Liu et al., 1993; Plesh et al., 1986). If cycle duration increases with food hardness, why does mandibular loading time not reliably predict mandibular loading magnitude during rhythmic chewing? Variation in cycle duration need not necessarily translate into consistent variation in the duration of mandibular loading if changes in cycle duration are due to changes in opening and closing phase exclusive of the slow close/power stroke (SC/PS) phase (e.g. Plesh et al., 1986). Moreover, although it has also been reported that increases in food hardness can be associated with increases in the duration of SC (Thexton and Hiimeae, 1997; Yamada and Yamamura, 1996), SC duration need not be highly correlated with the durations of mandible loading and bite force generation (Hylander et al., 1987). In essence, it is not necessary that jaw kinematics and jaw kinetics be closely coupled.

One necessary result of this apparent decoupling of mandible loading duration and chew cycle duration is that there must be variation in chew duty factor. In this study, chew duty factor did show significant correlations with strain magnitude in approximately 25% of experiments, but it did not explain significantly more variance in multiple regression models, and was usually not significantly related to strain magnitude when other variables were included. If some animals do increase chew duty factors when increasing strain magnitudes and bite forces (Yamada and Yamamura, 1996), it is not a strategy adopted consistently within or across the mammalian species examined here (cf. Weijs and De Jongh, 1977).

Several studies have shown that increases in food 'hardness' are associated with increases in EMG burst duration (Hidaka et al., 1997; Lavigne et al., 1987; Liu et al., 1993; Lund et al., 1998; Morimoto et al., 1989). On the basis of these EMG data, it might seem reasonable to hypothesize that variation in bite force magnitudes in mammals is significantly correlated with variation in the duration of force generation. However, in those studies in which test strips of increasing hardness or steel balls were introduced between the teeth during CRJMs, increases in chew cycle time and durations of muscle activity were also accompanied by increases in muscle activity amplitudes (Hidaka et al., 1997; Lavigne et al., 1987; Liu et al., 1993; Lund et al., 1998; Morimoto et al., 1989). Hidaka et al. also found that increases in bite force are not accompanied by increases in bite load duration, but only in load rate. Harder foods did not elicit significant increases in masseter burst duration [fig. 11 in Liu et al. (Liu et al., 1993)] although there were increases in burst amplitude, suggesting again that increases in rate of force development must be more important for increasing bite force magnitudes than duration of force development.

In sum, the data suggesting that increases in bite force during CRJMs are associated with increases in jaw closer muscle burst duration are quite limited, and are not obviously related to patterns of bite force modulation. Perhaps the most important question about these studies is whether force is modulated the same way during CRJMs in anesthetized animals as in mastication in awake, alert animals. These considerations

require that we turn our attention to data from chewing in awake, alert animals.

Data from rabbits during rhythmic chewing show that burst durations in superficial masseter (measured from onset to offset) are longer during chewing of raw rice, of intermediate duration during pellet chewing, and shortest when chewing bread (Kakizaki et al., 2002; Weijs and Dantuma, 1981; Yamada and Haraguchi, 1995; Yamada and Yamamura, 1996). In humans, increases in gum hardness are associated with increases in masseter muscle burst duration measured from onset to offset (Plesh et al., 1986). [Other studies reporting changes in EMG activity with food hardness integrate the activity over various time periods, so the effect of hardness on burst durations cannot be definitively assessed (Agrawal et al., 1998; Foster et al., 2006; Lassauzay et al., 2000; Peyron et al., 2002; Plesh et al., 1986).] In cats, foods more resistant to compression tests (raw beef *versus* cooked chicken) elicit higher EMG burst durations, amplitude and spikes per unit time in some adductor muscles and not others (Gorniak and Gans, 1980).

Although all of these studies report increases in overall EMG burst durations in association with increases in food hardness, they also report increases in burst amplitude. However, it is not clear that overall EMG burst durations are indicative of how muscle force is modulated during the loading phase, nor how this relates to bite force generation. Without explicitly considering the relationship between changing food hardness and the rate of muscle force recruitment during loading (estimated as amplitude/time from onset to peak), data on overall muscle burst duration do not contradict the hypothesized importance of rate-modulation of muscle and bite force.

Rate-modulation of bite force

Mandibular strain magnitudes are primarily increased by increasing the rate of loading, and only secondarily by increasing the duration of loading. Because variation in mandibular bone strain magnitudes is a reasonable proxy for variation in bite force (Hylander, 1986), these results suggest that bite force is modulated primarily by increases in rate of force development, and only to a lesser extent by increases in the duration of force development. These results expand on observations on rabbits reported previously. Bone strain recorded from the mandibular corpus of rabbits during mastication revealed that the highest bone strain magnitudes were during pellet chewing and the lowest with carrot chewing (Weijs and De Jongh, 1977). Pellet chewing was also associated with shorter absolute strain durations and longer cycle times, and hence shorter duty factors than during carrot chewing. This implies that the differences in strain magnitude between pellet and carrot chewing are accounted for by changes in strain rate. Subsequently it was shown that increasing vertically oriented muscle force (estimated from EMG) was also associated with increased rates of force development, rather than increased duration [fig. 14 in Weijs and Dantuma (Weijs and Dantuma, 1981)]. Transducer

measures of bite force at anterior molars in rabbits during CRJMs also reveal that bite force is increased by increases in rate and not in the duration of force development (Hidaka et al., 1997). The available data suggest that both mandibular corpus strain magnitudes and bite force magnitudes during mastication are achieved primarily by modulating the rate of force development.

This finding is congruent with current models of the orderly recruitment of motor units. In locomotor muscles, as the excitatory input to a pool of motor neurons increases, the small motor neurons, which innervate small motor units consisting of slow twitch fibers, are recruited first, followed by progressively larger motor neurons and motor units consisting of faster fiber types (Burke, 1994; Burke and Tsairis, 1974; Henneman and Olson, 1965; Henneman et al., 1965a; Henneman et al., 1965b; McPhedran et al., 1965; Mendell and Henneman, 1971; Wuerker et al., 1965). Moreover, although the effect varies by muscle, in postcranial muscles motor unit recruitment is more important than motor unit firing rate in modulating muscle force output at low output levels (Fournier and Sieck, 1988; Hennig and Lomo, 1987; Tansey et al., 1996). This suggests that at low force output levels, increases in muscle force during rhythmic locomotion are accompanied by increased rates of muscle force generation, as progressively faster motor units are recruited in progressively increasing proportions.

These motor unit recruitment principles also appear to be used by the masticatory system. In mammalian masticatory muscles, as in the locomotor muscles, force modulation at low force amplitudes appears to be predominantly *via* muscle fiber recruitment rather than rate modulation (Goldberg and Derfler, 1977; Hannam and McMillan, 1994; Scutter and Türker, 1998). Mammalian masticatory muscles are not uniform in their fiber types (Anapol and Herring, 2000; Herring, 1994; Maxwell et al., 1979; Wall et al., 2006; Wall et al., 2005), and a large number of studies suggest that smaller, slower motor units are recruited before larger, faster motor units (Clark et al., 1978; Desmedt and Godaux, 1979; Goldberg and Derfler, 1977; Lev-Tov et al., 1993; Lund et al., 1979; Miles and Türker, 1986; Miles et al., 1987; van Eijden and Turkawski, 2001; Van Wessel et al., 2005; Wall et al., 2006; Wall et al., 2005; Yemm, 1977). Thus, the evidence suggests that the generation of progressively higher bite forces during rhythmic mastication is achieved through increased recruitment of larger, faster motor units, resulting in increases in the rate of the generation of muscle force.

We note in passing that it is theoretically possible to explain rate-modulation of bite force with reference to the degree of synchrony of recruitment of whole muscles. The various jaw elevator muscles act asynchronously on the mandible during mastication, so increases in muscle force levels might be associated with increasing rate of force generation by increasing the temporal overlap in activity patterns of the jaw elevator muscles. This possibility can only be evaluated with EMG data, and this work is currently under way. However, it seems unlikely that this strategy is adopted as the asynchronous activity of the jaw adductor muscles is critical for achieving the

precise, three-dimensional movements of the mandible characteristic of mastication in the mammals studied here (Hylander and Johnson, 1994; Hylander et al., 1987; Weijs, 1994). Increasing overlap of jaw adductor muscle activity might be expected to result in decreases in the transverse component of jaw movement characteristic of mastication in herbivorous mammals (Hiimae, 1978; Hiimae and Crompton, 1985).

In sum, the principal mechanism by which mammals modulate bite force magnitudes during rhythmic mastication does not involve varying the time over which force is generated, either by increasing chew cycle time or chew duty factor. It must be emphasized that the results of this study do not exclude the possibility that increased bite force magnitudes are at least in part achieved by increases in the duration of force generation. However, it is clear that bite force is modulated primarily by variations in load rate, and only secondarily by variation in load duration.

We hypothesize that mammals do not use time-modulation of masticatory forces during rhythmic mastication because this would require variation in chew cycle time, and/or chew duty factor. The data presented here and elsewhere (Anderson et al., 2002; Weijs and De Jong, 1977) suggest that strain magnitude is only weakly correlated with chew cycle time. We suggest that significant variation in chew cycle time would be difficult to accommodate in the context of a central pattern generator producing rhythmic bursts of activity at a relatively constant frequency. We further hypothesize that rate modulation of masticatory force allows rhythmic movements to occur at a relatively constant frequency, with attendant advantages for motor control computation. Rate modulation of force production in other rhythmic behaviors, such as locomotion, may also be explained in the same way.

Unloading of the mandible during mastication

Across the mammals studied, it was also evident that strain magnitude was associated primarily with not only the rate at which the mandible is loaded during the power stroke, but also the rate at which it is unloaded. The rate and duration of jaw unloading are probably determined by the relaxation characteristics of the jaw elevator muscles (Hylander and Johnson, 1993; Hylander and Johnson, 1994; Hylander et al., 1987; Luschei and Goodwin, 1974), and these relaxation characteristics are in turn affected by the order of derecruitment of motor units. The order of motor unit derecruitment in masticatory muscles is, to our knowledge, unstudied. In locomotor muscles, motor units are derecruited in the inverse order to which they were recruited (i.e. large, fast motor units are derecruited first, followed by small slow motor units), so that more highly recruited muscles will show higher rates of force drop off after peak than less highly recruited muscles. If this derecruitment principle also applies in the masticatory muscles, the rate of force drop-off after peak will be positively related to the activity level of the muscle. Therefore, if the unloading behavior of the mandible is indeed primarily affected by the relaxation characteristics of the jaw elevator muscles

(Hylander and Johnson, 1993; Hylander and Johnson, 1994; Hylander et al., 1987; Luschei and Goodwin, 1974), it seems reasonable to hypothesize that the correlation between bone strain amplitude and strain unloading rate in the mandibular corpus reflects the orderly derecruitment of muscle fibers in the mammalian masticatory muscles.

Conclusions

The mandibular corpus bone strain data presented here suggest that across a broad range of mammals, mandibular loading, and presumably bite force, magnitudes during rhythmic mastication are modulated primarily by modulating the rate of loading, rather than by loading duration. This suggests that muscle force recruitment in the masticatory apparatus during rhythmic chewing might be achieved in a manner paralleling the locomotor system: i.e. small, slow motor units are recruited first, and increases in force are achieved by recruiting progressively faster and larger motor units. Modulation of strain and force generation in rhythmic mastication primarily by changes in load rate has the advantage of enabling chewing frequency to remain more or less constant. This might have the advantage of simplifying computational tasks associated with modulation. We do not argue that this is the only way that force can be modulated during chewing. Indeed, time-modulation of chewing forces might be an appropriate during isometric biting, when the internal material properties of foods are unknown or unpredictable, such as when chewing on bones (Oron and Crompton, 1985), or during the initial ingestive cycles of a chewing sequence. Comparison of force modulation during different feeding behaviors promises to provide insight into motor control strategies during feeding in vertebrates.

K.L.R.'s research was supported by NIDCR DE14457. S.W.H. and Z.-J.L.'s work was supported by DE 11962 from NIDCR to Herring; Scott Pedersen helped with their research. S.H.W.'s research was funded by NSF Dissertation Improvement (BCS-02-41652), NSF IOS-0520855, NSF BCS-01-38565 to W.L.H., Sigma-Xi Grant-in-Aid of Research, Aleanne Webb Dissertation Fellowship (Duke University), and the Ford Foundation. S.H.W. gratefully acknowledges assistance from C. Wall, C. Vinyard and K. Johnson during data collection. The alpacas were kindly lent to S.H.W. by D. Anderson, DVM. W.L.H.'s work was supported by NSF SBR-9420764, NIH DE-04531, and Duke University. M.J.R.'s work was supported by NIH DE-05595 and Duke University. W.L.H. and M.J.R. also acknowledge the assistance of K. Johnson with many aspects of their research. C.F.R.'s research was funded by NSF Physical Anthropology 97006676 and BCS-010913, made possible by the loan of animals from the Duke University Lemur Center, and was facilitated by B. Demes, S. Larson and J. Stern. K. Wasilewska assisted with data analysis. A poster presentation of this research was awarded the Nakamura Prize at the International Mastication Symposium in Brisbane, June 2006. This is Duke University Lemur Center Publication 1022.

References

- Agrawal, K. R., Lucas, P. W., Bruce, I. C. and Prinz, J. F. (1998). Food properties that influence neuromuscular activity during human mastication. *J. Dent. Res.* **77**, 1931-1938.
- Agrawal, K. R., Lucas, P. W. and Bruce, I. C. (2000). The effects of food fragmentation index on mandibular closing angle in human mastication. *Arch. Oral Biol.* **45**, 577-584.
- Ahlgren, J. (1976). Masticatory movements in primitive mammals. In *Mastication* (ed. D. J. Anderson and B. Matthews), pp. 119-130. Bristol: John Wright & Sons.
- Anapol, F. and Herring, S. (2000). Ontogeny of histochemical fiber types and muscle function in the masseter muscle of miniature swine. *Am. J. Phys. Anthropol.* **112**, 595-613.
- Anderson, K., Throckmorton, G. S., Buschang, P. H. and Hayasaki, H. (2002). The effects of bolus hardness on masticatory kinematics. *J. Oral Rehabil.* **29**, 689-696.
- Berry, W. D. and Feldman, S. (1985). *Multiple Regression in Practice*. Beverly Hills: Sage Publications.
- Blanksma, N. G. and Van Eijden, T. M. (1995). Electromyographic heterogeneity in the human temporalis and masseter muscles during static biting, open close excursions, and chewing. *J. Dent. Res.* **74**, 1318-1327.
- Blanksma, N. G., van Eijden, T. M., van Ruijven, L. J. and Weijis, W. A. (1997). Electromyographic heterogeneity in the human temporalis and masseter muscles during dynamic tasks guided by visual feedback. *J. Dent. Res.* **76**, 542-551.
- Burke, R. E. (1994). Physiology of motor units. In *Myology: Basic and Clinical*. Vol. 1 (ed. A. G. Engel and C. Franzini-Armstrong), pp. 464-483. New York: McGraw-Hill.
- Burke, R. E. and Tsairis, P. (1974). Correlation of physiological properties with histochemical characteristics in single muscle units. *Ann. N. Y. Acad. Sci.* **228**, 145-159.
- Buschang, P. H., Hayasaki, H. and Throckmorton, G. S. (2000). Quantification of human chewing cycle kinematics. *Arch. Oral Biol.* **45**, 461-474.
- Clark, R. W., Luschei, E. S. and Hoffman, D. S. (1978). Recruitment order, contractile characteristics, and firing patterns of motor units in the temporalis muscle in monkeys. *Exp. Neurol.* **61**, 31-52.
- Deban, S. M., O'Reilly, J. C. and Nishikawa, K. C. (2001). The evolution of the motor control of feeding in Amphibians. *Am. Zool.* **41**, 1280-1298.
- Desmedt, J. E. and Godaux, E. (1979). Recruitment patterns of single motor units in the human masseter muscle during brisk jaw clenching. *Arch. Oral Biol.* **24**, 171.
- Foster, K. D., Woda, A. and Peyron, M. A. (2006). Effect of texture of plastic and elastic model foods on the parameters of mastication. *J. Neurophysiol.* **95**, 3469-3479.
- Fournier, M. and Sieck, G. C. (1988). Mechanical properties of muscle units in the cat diaphragm. *J. Neurophysiol.* **59**, 1055-1066.
- Goldberg, L. J. and Derfler, B. (1977). Relationship among recruitment order, spike amplitude, and twitch tension of single motor units in human masseter muscle. *J. Neurophysiol.* **40**, 879-890.
- Gorniak, G. C. and Gans, C. (1980). Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). *J. Morphol.* **163**, 253-281.
- Hannam, A. G. and McMillan, A. S. (1994). Internal organization in the human jaw muscles. *Crit. Rev. Oral Biol. Med.* **5**, 55-89.
- Henneman, E. and Olson, C. B. (1965). Relations between structure and function in the design of skeletal muscles. *J. Neurophysiol.* **28**, 581-598.
- Henneman, E., Somjen, G. and Carpenter, D. O. (1965a). Excitability and inhibitory of motoneurons of different sizes. *J. Neurophysiol.* **28**, 599-620.
- Henneman, E., Somjen, G. and Carpenter, D. O. (1965b). Functional significance of cell size in spinal motoneurons. *J. Neurophysiol.* **28**, 560-580.
- Hennig, R. and Lomo, T. (1987). Gradation of force output in normal fast and slow muscles of the rat. *Acta Physiol. Scand.* **130**, 133-142.
- Herrel, A., Meyers, J. J., Nishikawa, K. C. and De Vree, F. (2001). The evolution of feeding motor patterns in lizards: modulatory complexity and possible constraints. *Am. Zool.* **41**, 1311-1320.
- Herring, S. (1994). Functional properties of the feeding musculature. In *Biomechanics of Feeding in Vertebrates*. Vol. 18 (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 5-30. Berlin: Springer-Verlag.
- Herring, S. W. and Teng, S. (2000). Strain in the braincase and its sutures during function. *Am. J. Phys. Anthropol.* **112**, 575-593.

- Hidaka, O., Morimoto, T., Masuda, Y., Kato, T., Matsuo, R., Inoue, T., Kobayashi, M. and Takada, K. (1997). Regulation of masticatory force during cortically induced rhythmic jaw movements in the anesthetized rabbit. *J. Neurophysiol.* **77**, 3168-3179.
- Hiimeae, K. (1978). Mammalian mastication: a review of the activity of jaw muscles and the movements they produce in chewing. In *Development, Function and Evolution of Teeth* (ed. P. M. Butler and K. Joysey), pp. 359-398. London: Academic Press.
- Hiimeae, K. M. and Crompton, A. W. (1985). Mastication, food transport, and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 262-290. Cambridge: Belknap Press.
- Hylander, W. L. (1977). In vivo bone strain in the mandible of *Galago crassicaudatus*. *Am. J. Phys. Anthropol.* **46**, 309-326.
- Hylander, W. L. (1979). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: an in vivo approach to stress analysis of the mandible. *J. Morphol.* **159**, 253-296.
- Hylander, W. L. (1986). In vivo bone strain as an indicator of masticatory bite force in *Macaca fascicularis*. *Arch. Oral Biol.* **31**, 149-157.
- Hylander, W. L. and Johnson, K. R. (1993). Modeling relative masseter force from surface electromyograms during mastication in non-human primates. *Arch. Oral Biol.* **38**, 233-240.
- Hylander, W. L. and Johnson, K. R. (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *Am. J. Phys. Anthropol.* **94**, 523-547.
- Hylander, W. L., Johnson, K. R. and Crompton, A. W. (1987). Loading patterns and jaw movements during mastication in *Macaca fascicularis*: a bone-strain, electromyographic, and cineradiographic analysis. *Am. J. Phys. Anthropol.* **72**, 287-314.
- Hylander, W. L., Ravosa, M. J., Ross, C. F. and Johnson, K. R. (1998). Mandibular corpus strain in primates: further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. *Am. J. Phys. Anthropol.* **107**, 257-271.
- Kakizaki, Y., Uchida, K., Yamamura, K. and Yamada, Y. (2002). Coordination between the masticatory and tongue muscles as seen with different foods in consistency and in reflex activities during natural chewing. *Brain Res.* **929**, 210-217.
- Lassauzay, C., Peyron, M.-A., Albuissou, E., Dransfield, E. and Woda, A. (2000). Variability of the masticatory process during chewing of elastic model foods. *Eur. J. Oral Sci.* **108**, 484-492.
- Lavigne, G., Kim, J. S., Valiquette, C. and Lund, J. P. (1987). Evidence that periodontal pressoreceptors provide positive feedback to jaw closing muscles during mastication. *J. Neurophysiol.* **58**, 342-358.
- Lev-Tov, A., Tal, M. and Lavy, R. (1993). Diverse firing properties of single motor units in the inner and outer portions of the guinea pig anterior digastric muscle. *Arch. Oral Biol.* **38**, 169.
- Liu, Z. J. and Herring, S. E. (2000a). Bone surface strains and internal bony pressures at the jaw joint of the miniature pig during masticatory muscle contraction. *Arch. Oral Biol.* **45**, 95-112.
- Liu, Z. J. and Herring, S. E. (2000b). Masticatory strains on osseous and ligamentous components of the temporomandibular joint in miniature pigs. *J. Orofac. Pain* **14**, 265-278.
- Liu, Z. J., Masuda, Y., Inoue, T., Fuchihata, H., Sumida, A., Takada, K. and Morimoto, T. (1993). Coordination of cortically induced rhythmic jaw and tongue movements in the rabbit. *J. Neurophysiol.* **69**, 569-584.
- Liu, Z. J., Ikeda, K., Harada, S., Kasahara, Y. and Ito, G. (1998). Functional properties of jaw and tongue muscles in rats fed a liquid diet after being weaned. *J. Dent. Res.* **77**, 366-376.
- Liu, Z. J., Green, J. R., Moore, C. A. and Herring, S. W. (2004). Time series analysis of jaw muscle contraction and tissue deformation during mastication in miniature pigs. *J. Oral Rehabil.* **31**, 7-17.
- Lund, J. P., Smith, A. M., Sessle, B. J. and Murakami, T. (1979). Activity of trigeminal alpha- and gamma-motoneurons and muscle afferents during performance of a biting task. *J. Neurophysiol.* **42**, 710-725.
- Lund, J. P., Kolta, A., Westberg, K. G. and Scott, G. (1998). Brainstem mechanisms underlying feeding behaviors. *Curr. Opin. Neurobiol.* **8**, 718-724.
- Lundgren, D. and Laurell, L. (1986). Occusal force pattern during chewing and biting in dentitions restored with fixed bridges of cross-arch extension. *J. Oral Rehabil.* **13**, 57-71.
- Luschei, E. S. and Goodwin, G. M. (1974). Patterns of mandibular movement and jaw muscle activity during mastication in the monkey. *J. Neurophysiol.* **37**, 954-966.
- Maxwell, L. C., Carlson, D. S., McNamara, J. A. and Faulkner, J. A. (1979). Histochemical characteristics of the masseter and temporalis muscles of the rhesus-monkey (*Macaca-Mulatta*). *Anat. Rec.* **193**, 389-401.
- McPhedran, A. M., Wuerker, R. B. and Henneman, E. (1965). Properties of motor units in a homogeneous red muscle (soleus) of the cat. *J. Neurophysiol.* **28**, 71-84.
- Mendell, L. M. and Henneman, E. (1971). Terminals of single Ia fibers: location, density, and distribution within a pool of 300 homonymous motoneurons. *J. Neurophysiol.* **34**, 171-187.
- Mericske-Stern, R., Geering, A. H., Bürgin, W. B. and Graf, H. (1992). Three-dimensional force measurements on mandibular implants supporting overdentures. *Int. J. Oral Maxillofac. Implants* **7**, 185-194.
- Miles, T. S. and Türker, K. S. (1986). Does reflex inhibition of motor units follow the "size principle"? *Exp. Brain Res.* **62**, 443.
- Miles, T. S., Türker, K. S. and Nordstrom, M. A. (1987). Reflex responses of motor units in human masseter muscle to electrical stimulation of the lip. *Exp. Brain Res.* **65**, 331-336.
- Morimoto, T., Inoue, T., Masuda, Y. and Nagashima, T. (1989). Sensory components facilitating jaw-closing muscle activities in the rabbit. *Exp. Brain Res.* **76**, 424-440.
- Nakajima, J., Hideshima, M., Takahashi, M., Taniguchi, H. and Takashi, O. (2001). Masticatory mandibular movements for different food textures related to onomatopoeic words. *J. Med. Dent. Sci.* **48**, 121-129.
- Oron, U. and Crompton, A. W. (1985). A cineradiographic and electromyographic study of mastication in *Tenrec ecaudatus*. *J. Morphol.* **185**, 155-182.
- Ottenhoff, F. A., van der Bilt, A., van der Glas, H. W. and Bosman, F. (1992). Control of elevator muscle activity during simulated chewing with varying food resistance in humans. *J. Neurophysiol.* **68**, 933-944.
- Ottenhoff, F. A. M., van der Bilt, A., van der Glas, H. W. and Bosman, F. (1993). Control of human jaw elevator muscle activity during simulated chewing with varying bolus sizes. *Exp. Brain Res.* **96**, 501-512.
- Ottenhoff, F. A. M., van der Bilt, A., van der Glas, H. W., Bosman, F. and Abbink, J. H. (1996). The relationship between jaw elevator muscle surface electromyogram and simulated food resistance during dynamic condition in humans. *J. Oral Rehabil.* **23**, 270-279.
- Peyron, M., Lassauzay, C. and Woda, A. (2002). Effects of increased hardness on jaw movement and muscle activity during chewing of viscoelastic model foods. *Exp. Brain Res.* **142**, 41-51.
- Plesh, O., Bishop, B. and McCall, W. (1986). Effect of gum hardness on chewing pattern. *Exp. Neurol.* **92**, 502-512.
- Proschel, P. and Hofmann, M. (1988). Frontal chewing patterns of the incisor point and their dependence on resistance of food and type of occlusion. *J. Prosthet. Dent.* **59**, 617.
- Ravosa, M. J., Johnson, K. R. and Hylander, W. L. (2000). Strain in the galago facial skull. *J. Morphol.* **245**, 51-66.
- Riebold, T. W., Gieser, D. R. and Goble, D. O. (1995). *Large Animal Anesthesia: Principles and Techniques*. Ames: Blackwell.
- Ross, C. and Hylander, W. L. (1996). In vivo and in vitro bone strain in owl monkey circumorbital region and the function of the postorbital septum. *Am. J. Phys. Anthropol.* **101**, 183-215.
- Scutter, S. D. and Türker, K. S. (1998). Recruitment stability in masseter motor units during isometric voluntary contractions. *Muscle Nerve* **21**, 1290-1298.
- Sessle, B. J. (2006). Mechanisms of oral somatosensory and motor functions and their clinical correlates. *J. Oral Rehabil.* **33**, 243-261.
- Tansey, K. E., Yee, A. K. and Botterman, B. R. (1996). Activation of type-identified motor units during centrally evoked contractions in the cat medial gastrocnemius muscle. III. Muscle-unit force modulation. *J. Neurophysiol.* **75**, 51-59.
- Thexton, A. and Hiimeae, K. M. (1997). The effect of food consistency upon jaw movement in the macaque: a cineradiographic study. *J. Dent. Res.* **76**, 552-560.
- Thomason, J. J., Grovum, L. E., Deswysen, A. G. and Bignell, W. W. (2001). In vivo surface strain and stereology of the frontal and maxillary bones of sheep: Implications for the structural design of the mammalian skull. *Anat. Rec.* **264**, 325-338.
- Trulsson, M. (2006). Sensory-motor function of human periodontal mechanoreceptors. *J. Oral Rehabil.* **33**, 262-273.
- Tsuboi, A., Kolta, A., Chen, C. C. and Lund, J. P. (2003). Neurons of the trigeminal main sensory nucleus participate in the generation of rhythmic motor patterns. *Eur. J. Neurosci.* **17**, 229-238.
- van Eijden, T. M. and Turkawski, S. J. (2001). Morphology and physiology of masticatory muscle motor units. *Crit. Rev. Oral Biol. Med.* **12**, 76-91.
- Van Wessel, T., Langenbach, G. E. J., Korfage, J. A. M., Brugman, P.,

- Kawai, N., Tanaka, E. and Van Eijden, T. M. G. J. (2005). Fibre-type composition of rabbit jaw muscles is related to their daily activity. *Eur. J. Neurosci.* **22**, 2783-2791.
- Wall, C. E., Vinyard, C., Johnson, K. R., Williams, S. H. and Hylander, W. L. (2005). Functional heterogeneity of the temporalis muscle of male and female baboons. *Am. J. Phys. Anthropol. Suppl.* **40**, 217.
- Wall, C. E., Briggs, M., Schachar, F., Vinyard, C., Williams, S. H. and Hylander, W. L. (2006). Anatomical and functional specializations of the anterior temporalis muscle of baboons. *Comp. Biochem. Physiol.* **134A**, S70.
- Weijs, W. A. (1994). Evolutionary approach to masticatory motor patterns in mammals. In *Advances in Comparative and Environmental Physiology*. Vol. 18 (ed. V. Bels, M. Chardon and P. Vandewalle), pp. 281-320. Berlin, Heidelberg: Springer-Verlag.
- Weijs, W. A. and Dantuma, R. (1981). Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus* L.). *Neth. J. Zool.* **31**, 99-147.
- Weijs, W. A. and De Jong, J. H. (1977). Strain in mandibular alveolar bone during mastication in the rabbit. *Arch. Oral Biol.* **22**, 667-675.
- Westberg, K. G., Scott, G., Olsson, K. A. and Lund, J. P. (2001). Discharge patterns of neurons in the medial pontobulbar reticular formation during fictive mastication in the rabbit. *Eur. J. Neurosci.* **14**, 1709-1718.
- Williams, S. H. (2004). Mastication in selenodont artiodactyls: an in vivo study of masticatory form and function in goats and alpacas. PhD thesis, Department of Biological Anthropology and Anatomy, Duke University, Durham, USA.
- Wuerker, R. B., McPhedran, A. M. and Henneman, E. (1965). Properties of motor units in a heterogeneous pale muscle (M. gastrocnemius) of the cat. *J. Neurophysiol.* **28**, 85-99.
- Yamada, Y. and Haraguchi, N. (1995). Reflex changes in the masticatory muscles with load perturbations during chewing hard and soft food. *Brain Res.* **669**, 86-92.
- Yamada, Y. and Yamamura, K. (1996). Possible factors which may affect phase durations in the natural chewing rhythm. *Brain Res.* **706**, 237-242.
- Yemm, R. (1977). The orderly recruitment of motor units of the masseter and temporal muscles during voluntary isometric contraction in man. *J. Physiol. Lond.* **265**, 163-174.