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RESEARCH ARTICLE

Jaw kinematics and tongue protraction–retraction during chewing and drinking in the pig

Rachel A. Olson[1,*], Stéphane J. Montuelle[2], Brad A. Chadwell[3], Hannah Curtis[4] and Susan H. Williams[4]

ABSTRACT

Mastication and drinking are rhythmic and cyclic oral behaviors that require interactions between the tongue, jaw and a food or liquid bolus, respectively. During mastication, the tongue transports and positions the bolus for breakdown between the teeth. During drinking, the tongue aids in ingestion and then transports the bolus to the oropharynx. The objective of this study was to compare jaw and tongue kinematics during chewing and drinking in pigs. We hypothesized there would be differences in jaw gape cycle dynamics and tongue protraction–retraction between behaviors. Mastication cycles had an extended slow-close phase, reflecting tooth–food–tooth contact, whereas drinking cycles had an extended slow-open phase, corresponding to tongue protrusion into the liquid. Compared with chewing, drinking jaw movements were of lower magnitude for all degrees of freedom examined (jaw protraction, yaw and pitch), and were bilaterally symmetrical with virtually no yaw. The magnitude of tongue protraction–retraction (Tx_t), relative to a mandibular coordinate system, was greater during mastication than during drinking, but there were minimal differences in the timing of maximum and minimum Tx_t relative to the jaw gape cycle between behaviors. However, during drinking, the tongue tip is often located outside the oral cavity for the entire cycle, leading to differences between behaviors in the timing of anterior marker maximum Tx_t. This demonstrates that there is variation in tongue–jaw coordination between behaviors. These results show that jaw and tongue movements vary significantly between mastication and drinking, which hints at differences in the central control of these behaviors.

KEY WORDS: XROMM, Mastication, Sucking, Rhythmicity, Movement

INTRODUCTION

Feeding and drinking are essential oral behaviors that provide organisms with the necessary nutrients, energy and hydration for survival. In most mammals, mastication, or chewing, is an important component of feeding because it creates a safely swallowable bolus. Mastication involves interactions among occlusal surfaces of opposing upper and lower postcanine teeth and the food. In contrast, in adult mammals, the primary methods of active liquid ingestion – lapping, licking and sucking – are tongue- or lip-based behaviors involving no intentional interactions between the bolus and the teeth. Lapping is commonly used by mammals with incomplete cheeks whereas sucking is used by mammals with complete cheeks. During lapping, the tongue protrudes into the liquid, but the lips are not submerged (Crompton and Musinsky, 2011; Reis et al., 2010; Thexton and Crompton, 1989; Thexton and McGarrick, 1988). When the tongue contacts a solid surface with lapping-like movements, the liquid is ingested by licking (Weijnen, 1998). During sucking, the lips are completely submerged into the liquid and liquid transport is achieved through changes in intraoral pressure (Thexton et al., 1998).

Despite these fundamental differences, mastication and drinking are both accomplished by coordinated and rhythmic movements of the tongue and jaw controlled by the central and peripheral nervous systems. A central pattern generator (CPG) in the brainstem drives masticatory rhythm (Dellow and Lund, 1971; Nozaki et al., 1986). The output of the masticatory CPG is modulated by feedback from the periodontal ligaments, jaw and orofacial muscle spindles, and tongue mechanoreceptors in order to correctly position food for processing and adjust force output (Lund and Kolta, 2005, 2006; Takahashi et al., 2007; Trulsson, 2007; Trulsson and Johansson, 2002). Although extensive modulation of the CPG adjusts movements as the food is chewed (e.g. Davis, 2014; Dotsch and Dantuma, 1989; Iriarte-Diaz et al., 2011; Thexton and Crompton, 1989; Weijs and De Jongh, 1977), gape cycles during mastication are highly rhythmic (Ross et al., 2007a,b, 2010, 2017). Similar CPGs regulating rhythmicity have been observed for licking, lapping and sucking (Barlow, 2009; Boughter et al., 2012; Nakamura et al., 1999; Travers et al., 1997), but with contributions from different cortical areas than for mastication (Iriki et al., 1988). While less studied, there is evidence to suggest that modulation of the CPG involved in drinking also occurs. For example, licking frequency in rats is influenced by experimental and environmental conditions (Weijnen, 1998).

Whereas there is a general understanding of the changes in CNS connections between cortical and brainstem areas underlying the maturation from drinking in infants (i.e. suckling) to chewing (Iriki et al., 1988), as well as the kinematic changes across this shift (German et al., 1992, 2006; German and Crompton, 1996, 2000; Westneat and Hall, 1992), comparatively less is known about the differences and similarities between mastication and non-suckling drinking kinematics and motor control. Studies on the cat (Hiiemae et al., 1978; Thexton and McGarrick, 1988, 1989) and the opossum (Crompton, 1989) have compared jaw and tongue movements during mastication and lapping but only one study, on pigs, has compared mastication and sucking in behaviorally mature animals (Liu et al., 2009). This study, however, focused specifically on tongue internal deformations rather than positional changes relative to the oral cavity.

These previous comparisons demonstrate that during mastication, the tongue positions the bolus along the toothrow for processing,

[1]Ohio University, Department of Biological Sciences, Irvine Hall 107, Athens, OH 45701, USA. [2]Ohio University Heritage College of Osteopathic Medicine, Department of Biomedical Sciences, 4180 Warrensville Center Road, SPS121, Warrensville Heights, OH 44122, USA. [3]Idaho College of Osteopathic Medicine, 1401 E. Central Dr., Meridian, ID 83642, USA. [4]Ohio University Heritage College of Osteopathic Medicine, Department of Biomedical Sciences, Irvine Hall 228, Athens, OH 45701, USA.

*Author for correspondence (rachel.olson.phd@gmail.com)

R.A.O., 0000-0003-0803-9519; S.J.M., 0000-0002-8638-9779; B.A.C., 0000-0002-8345-212X; S.H.W., 0000-0003-4167-678X

Received 21 October 2020; Accepted 19 February 2021

Journal of Experimental Biology (2021) 224, jeb239509. doi:10.1242/jeb.239509

usually unilaterally. When the jaw begins opening, the tongue protrudes to collect the food particles before retracting to reposition the bolus on the occlusal surface at the beginning of closing (Crompton, 1989; Hiiemae et al., 1978). When lapping, the tongue also protrudes during early opening and then retracts later during opening, trapping the aliquot between the tongue and hard palate prior to the next cycle (Crompton, 1989; Crompton and Musinsky, 2011; Gart et al., 2015; Hiiemae et al., 1978; Reis et al., 2010; Thexton and McGarrick, 1988; Thexton and Crompton, 1989). During drinking in pigs, the tongue extends into the liquid with the snout immersed, suggesting that the tongue may assist during sucking to bring the liquid into the oral cavity (German and Crompton, 2000; Thexton et al., 1998). Nevertheless, tongue movements serve distinct functions during these two behaviors – bolus placement and positioning within the oral cavity during mastication and bolus transport into and through the oral cavity to the oropharynx during drinking. This suggests that there may be behavior-dependent coordination patterns between the tongue and the jaw, particularly when viewed in the context of differences in jaw movements and overall gape cycle dynamics.

The goal of the present study was to compare jaw and tongue kinematics during mastication and drinking in the pig (*Sus scrofa* Linnaeus 1758) using X-ray reconstruction of moving morphology (XROMM) with additional soft tissue markers in the tongue. First, we determined whether the two behaviors use the same degrees of freedom during their respective gape cycles. Previous studies have demonstrated that two rotations, jaw pitch and jaw yaw, and anteroposterior translation (i.e. jaw protraction–retraction) are used during mastication (Brainerd et al., 2010; Menegaz et al., 2015; Montuelle et al., 2020a). Whereas jaw pitch reflects jaw opening and closing, jaw yaw reflects rotation about a vertical axis contributing to the characteristic 'sidedness' of mastication. We hypothesized that the two behaviors utilize similar magnitudes of jaw pitch and anteroposterior translation, but that jaw yaw will be absent during drinking because no sided interaction between the teeth and the aliquot occurs.

Second, we compared the temporal dynamics of gape cycles during the two behaviors. We hypothesized that masticatory cycles are longer and more variable than drinking cycles, reflecting the changing properties of the bolus throughout a chewing sequence. This variability is expected to extend to intracycle phases (e.g. fast closing, slow closing). Additionally, we hypothesized that the jaw opening phases of drinking cycles will be longer than those of masticatory cycles because of pronounced extraoral excursions of the anterior tongue during jaw opening.

Finally, we compared protraction and retraction movements of the tongue during chewing and drinking and related these movements to the temporal dynamics of the gape cycle. We hypothesized that drinking involves higher magnitudes of tongue protraction–retraction than chewing in order to ingest and transport liquid to the oropharynx. However, because injury to the tongue can occur if jaw and tongue movements are not coordinated (Montuelle et al., 2019, 2020b), we hypothesized that the timing of protraction and retraction relative to the gape cycle is similar between the two behaviors and has low variability.

By comparing jaw and tongue movements during mastication and drinking, this study provides a better understanding of the dynamic control of oral behavior variation driven by interactions between central (e.g. CPGs, premotor cortex, sensorimotor cortex) and peripheral (e.g. orofacial mechanoreceptors) components of the nervous system. Because mammals exhibit two types of rhythmic drinking behavior throughout their lifespan (i.e. suckling and either lapping, licking or sucking), any similarities in the kinematics of mastication and drinking in weaned animals may indicate more overlap in some aspects of the central control of these behaviors or similarities in their modulation, despite differences in bolus properties or position.

MATERIALS AND METHODS

Study design, surgery, CT scans and data collection

Jaw movements in two 3 month old female Hampshire-cross pigs (ID 20 and 21) were quantified using marker-based XROMM (Brainerd et al., 2010). In each animal, 5–7 radiopaque tantalum markers (1.6 mm diameter; Bal-Tec, Los Angeles, CA, USA) were surgically implanted in the skull and jaw while animals were under isoflurane anesthesia (2–5%). An additional 17 markers were placed in the tongue, with only the anterior and posterior markers used in this study (see below). After a minimum recovery period of 1 week, biplanar fluoroscopy videos were recorded at 250 frames s^{-1} using synchronized high-speed digital cameras (Oqus 310, Qualisys, Göteborg, Sweden) while the animals were feeding or drinking. Trials used in this study were of good quality, were recorded at least a week after initial implantation (to allow the markers to settle/scar into the soft tissues) and, when possible, were closest to the euthanasia date as possible to minimize these effects. During recording sessions, animals were offered 2 cm×2 cm×1 cm cubes of apple or 475 ml of apple juice. Prior to each session, perforated metal sheets (part number 9255T641, McMaster-Carr, Robinson, NJ, USA) and a custom Lego® calibration cube were imaged in each fluoroscopy view to aid in undistorting and calibrating the videos, respectively, following the standard XROMM workflow (Brainerd et al., 2010; Knorlein et al., 2016; Menegaz et al., 2015). Average radiation exposure settings were 100 kVp and 4.3 mA.

After marker implantation, the animals were CT scanned at The Ohio State University College of Veterinary Medicine (Columbus, OH, USA) on a GE Lightspeed Ultra CT scanner while under isoflurane anesthesia (2–5%). These scans were used to create the bone models necessary to produce the XROMM animations. Once data collection was complete, a post-mortem CT scan was performed at Holzer Clinic (Athens, OH, USA) on a Philips Brilliance 64 scanner for the precision study. Meshes of bones from the CT scans were created in VGSTUDIO MAX 3.3 (Volume Graphics GmbH). All procedures were approved by the Ohio University Institutional Animal Care and Use Committee (protocol #12-U-009).

XROMM study and data analysis

XMALab (version 1.5.4; Knorlein et al., 2016) was used to perform calibrations, undistort the individual fluoroscopy videos for each sequence, track undistorted marker coordinates in each undistorted and calibrated fluoroscopic view, calculate 3D coordinates of each marker, and reconstruct rigid body transformations, which were filtered using a low-pass Butterworth filter with a cut-off frequency of 25 Hz. In short, the perforated metal sheet was imaged to determine distortions in the field of view whereas the calibration cube was imaged in multiple positions across the field in order to determine the camera position, orientation, and spacing. As this gives orientation and scale to the field of view, marker screen coordinates can then be translated to calibrated 3D space.

A joint coordinate system (JCS) was created in Maya (Autodesk Inc., San Rafael, CA, USA) using the CT reconstruction of the skull and jaw and then used to calculate rotations and translations of the jaw relative to the skull. All axes are perpendicular to each other with the *x*-axis running anteroposterior in the midline, the *y*-axis

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oriented dorsoventrally, and the *z*-axis oriented along the mediolateral plane running through both condyles (Fig. 1A). Both a translation (T) and a rotation (R) is possible about each of these axes, creating a potential for six degrees of freedom (DoF) describing rigid body kinematics: Tx, Ty, Tz, Rx, Ry, Rz.

Displacement of the tongue markers was measured relative to a jaw anatomical coordinate system (ACS) (Fig. 1B). This system was a more ventrally positioned coordinate system, with the *xy*- and *yz*-planes in line with the JCS used to calculate rigid body translations and rotations, but with the *xz*-plane shifted dorsally so that it is positioned along the hard palate. This allows for the calculation of movements of the anterior and posterior tongue markers (Fig. 1C) relative to the jaw while eliminating the influence of gape on translation in the *x*-dimension. Unadjusted tongue marker Tx_t values (anteroposterior translation: protraction–retraction) indicate displacement relative to the jaw ACS. Additionally, Tx_t of the anterior tongue marker was also adjusted so that the tip of the right central incisor defined the zero-position in the *x*-dimension (Fig. 1C). Positive adjusted Tx_t values indicate the anterior tongue marker is located outside the oral cavity, whereas negative adjusted Tx_t values indicate that it is located within the oral cavity, with the oral cavity being defined consistent with the human anatomical nomenclature in being bound anteriorly and on the sides by the dentition. Therefore, positive adjusted Tx_t values are outside the oral cavity but may still be within the space between the teeth and soft tissues surrounding the oral opening (i.e. the oral vestibule).

After euthanasia, the frozen head of each animal was imaged within the calibrated c-arm space. Movements of the markers were then analyzed following the same XROMM workflow as above. These videos were used to calculate precision thresholds for each of the 6 DoF of rigid body motion (3 translations and 3 rotations about each of the 3 JCS axes). As no movement between the skull and the jaw is expected in the frozen specimen, any change quantified in any DoF is interpreted as digitizing error and/or error in the data collection workflow, such as suboptimal bead placement. The sequence mean of each DoF plus or minus the precision value for each individual determines the threshold for determining jaw movements that exceed error and thus can be interpreted as real biological motion. Precision thresholds for each animal are provided in Table S1.

Waves representing the DoF that exceeded the precision thresholds, along with waves representing tongue protraction–retraction were then analyzed in a custom-written MATLAB script

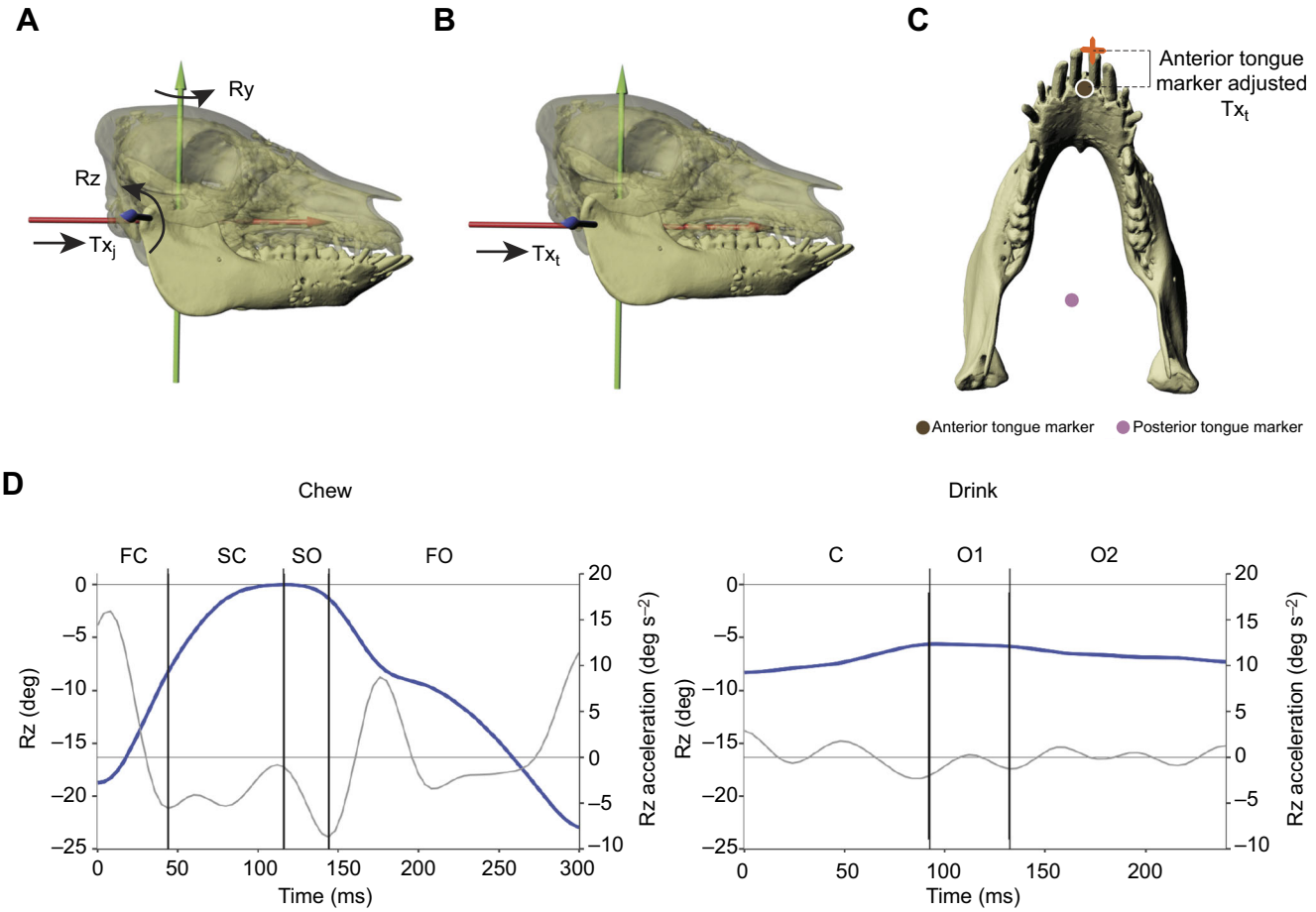

Fig. 1. Jaw and tongue coordinate systems and tongue marker locations. (A) Orientation of the temporomandibular joint coordinate system for characterizing jaw movement (Tx_j, jaw protraction–retraction), (B) orientation of the anatomical coordinate system relative to the jaw used for characterizing tongue protraction–retraction (i.e. Tx_t), and (C) locations of the anterior (brown) and posterior (pink) tongue markers relative to the jaw at rest. Adjusted Tx_t values for the anterior tongue marker are corrected relative to the tip of the right lower incisor (orange cross). Positive Tx_t values indicate that the anterior marker is outside the oral cavity and negative Tx_t values indicate that the marker is inside the oral cavity. (D) Graph of jaw pitch (Rz, blue) and rotational acceleration (gray) during representative chewing (left) and drinking (right) cycles from pig ID 21 showing the differences in intracycle phases between the two behaviors. Phases for each type of cycle are based on the acceleration and directionality of Rz. FC, fast close; SC, slow close; SO, slow open; FO, fast open; C, close, O1, open 1; O2, open 2.

(FeedCycle: available from Dr Brad Chadwell, Idaho College of Osteopathic Medicine, bchadwell@idahocom.org) that uses Rz (jaw pitch), the second derivative of Rz (jaw pitch acceleration) and Ry (jaw yaw) to identify key parameters of individual gape cycles automatically. Individual cycles were defined from one instance of minimum Rz (i.e. maximum gape) to the following instance of minimum Rz. Within each cycle, maximum Rz (i.e. minimum gape) was used to determine the transition from jaw close to jaw open. The maximum negative value (i.e. deceleration) of the second derivative of Rz was then used to divide opening and closing into its constituent phases: fast close (FC), slow close (SC), slow open (SO) and fast open (FO). The partitioning of gape cycles into phases based on the acceleration of Rz revealed differences between mastication and drinking that impacted subsequent analysis (Fig. 1D). The four standard phases were observed in chewing cycles (i.e. FC, SC, SO and FO), whereas only three phases were detected in drinking cycles: one closing phase (C) and 2 opening phases (hereafter called O1 and O2) (Fig. 1D). Because of these differences, we compared the phases between behaviors corresponding in the directionality (i.e. opening or closing) and acceleration of Rz. Thus, FC of mastication was compared with the single closing phase of drinking because of the comparable velocity of jaw closing. For opening, phases were compared based on their order of occurrence, i.e. SO and FO were compared with O1 and O2, respectively, given their presumed functionality in the context of the gape cycle.

For each cycle, total cycle duration and relative phase duration (expressed as a percentage of total gape cycle duration) were calculated. For each DoF, maximum magnitudes within each cycle and phase were calculated as the difference between the maximum and minimum values of a DoF and are reported as absolute values. Magnitudes reflect the main movements that occur within a time frame (cycle or phase) for that DoF.

In the feeding dataset used for statistical analysis, we eliminated non-chewing cycles (e.g. ingestion, stage I transport) and dropped all cycles containing a visible swallow. This resulted in 47 masticatory cycles and 40 drinking cycles for pig ID 20, and 55 masticatory and 50 drinking cycles for pig ID 21. All statistical analyses were performed in R version 3.6.1 (http://www.R-project.org/). For magnitude variables, we used linear mixed effects models with repeated measures, with behavior as a fixed factor and individual as the random factor using the lme (R package version 3.1-143; https://CRAN.R-project.org/package=nlme) and emmeans (R package version 1.5.1; https://CRAN.R-project.org/package=emmeans) functions. Additionally, in order to compare variability in cycle duration, the coefficient of variation (CV) was calculated for each cycle and phase within each sequence of mastication or drinking. Mean and variance of timing parameters were calculated with the CircStats package (R package version 0.2-6; https://CRAN.R-project.org/package=CircStats). For timing parameter models, we used Bayesian circular mixed effects models with repeated measures, with behavior as a fixed factor and individual as the random factor using the bpnme function (10,000 iterations, 2000 burn-in, 101 seed, *n*.lag=3) from the package bpnreg (R package version 1.0.3; https://CRAN.R-project.org/package=bpnreg) following the methods of Cremers and Klugkist (2018). This method produces the posterior mean, posterior standard deviation and the 95% highest posterior density (HPD) interval. HPDs (Fig. S1) are reported as the start position (percentage cycle duration) to end position, where directionality matters. Non-overlapping HPDs indicate a difference between behaviors whereas overlapping HPDs indicate that the null hypothesis of no differences between behaviors cannot be rejected.

RESULTS

Jaw movements and cycle dynamics

Jaw movements during rhythmic mastication exceeded precision thresholds for only three of the six potential DoF: rotation about the *z*-axis (Rz: jaw pitch) and *y*-axis (Ry: jaw yaw), as well as translation along the *x*-axis (Tx_j: protraction–retraction) (Fig. S2). Ty and Tz occasionally exceeded precision thresholds but were of much smaller magnitude than Tx_j and did not show a rhythmic pattern relative to the gape cycle. Instead, this most likely indicates noise above our precision threshold rather than true movement. In contrast, jaw movements during drinking cycles only exceeded precision thresholds for Rz and Tx_j (Fig. S2). This reveals that, as hypothesized, jaw yaw (Ry) does not exceed precision values during drinking, and therefore, is not a significant movement during this behavior.

Compared with values for drinking, the magnitudes of Rz, Ry and Tx_j were significantly greater during mastication for whole cycles and each intracycle phase (Table 1). During both behaviors, the jaw reached maximum Rz (i.e. minimum gape) approximately 40% into the cycle (Fig. 2A). Jaw yaw (Ry) reached a maximum just after minimum gape during mastication, at which point it reset for the next cycle by switching yaw direction (Fig. 2B). In contrast, Ry lacked a discernible peak during drinking, indicating that it is a bilaterally symmetrical behavior, unlike mastication. For both behaviors, jaw retraction (i.e. decreasing Tx_j) occurred during jaw closing whereas protraction (i.e. increasing Tx_j) occurred during opening (Fig. 2C).

Masticatory cycles were significantly longer than drinking cycles (Table 1). Comparison of phases revealed that the absolute duration of C during drinking was significantly longer than the corresponding FC of mastication, but more closely corresponded to the total duration of FC+SC of mastication. Contrary to our hypothesis for jaw opening, SO and O1 absolute duration did not differ between the two behaviors, but FO (chewing) was significantly longer than O2 (drinking). Variability, as indicated by the CV (see Table 1), in average cycle duration across all sequences was lower for mastication (9.50) than for drinking (29.1) contrary to our prediction. At the phase level, however, opening phases were more variable than closing phases for both behaviors.

The relative contribution of each phase to total gape cycle duration also differed between the two behaviors (Table 1). Whereas C and O1 were proportionately longer for drinking cycles than FC and SO, respectively, FO had a higher contribution to total cycle duration for chewing cycles than O2 did for drinking cycles (Fig. S3). Higher variability in relative phase duration was also observed for opening phases of both chewing and drinking cycles relative to closing phases (Table 1).

Tongue protraction–retraction

The timing of protraction and retraction of the anterior and posterior tongue markers was generally similar within a behavior relative to each other and relative to changes in jaw pitch but differences were observed between behaviors (Fig. 3). During chewing, the anterior marker had minimal movement during jaw closing, then protracted at the start of jaw opening, followed by retraction as the jaw opened to maximum gape (Fig. 3A). In contrast, the posterior marker during chewing was already in the process of retracting as the jaw began to close from maximum gape. It then reached minimum retraction near minimum gape, and subsequently changed direction to reach maximum protraction part of the way through opening, before it

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Table 1. Cycle and phase level data for jaw movement and temporal dynamics during chewing and drinking cycles and corresponding model results

	Chew	Drink	Model
Magnitude			
Total cycle			
Rz (deg)	20.8±2.35	3.2±1.22	s.e.=0.276, $T_{2,192}$=64.2, P<0.0001
Ry (deg)	3.7±0.79	0.7±0.26	s.e.=0.0859, $T_{2,192}$=34.3, P<0.0001
Tx_j (mm)	7.0±1.25	2.1±0.41	s.e.=0.117, $T_{2,192}$=42.0, P<0.0001
FC/CI			
Rz (deg)	13.7±3.27	2.9±1.18	s.e.=0.365, $T_{2,192}$=29.6, P<0.0001
Ry (deg)	1.3±0.52	0.6±0.28	s.e.=0.0609, $T_{2,192}$=11.4, P<0.0001
Tx_j (mm)	4.3±1.58	1.9±0.59	s.e.=0.159, $T_{2,192}$=15.3, P<0.0001
SC			
Rz (deg)	6.3±2.74	–	–
Ry (deg)	1.2±0.79	–	–
Tx_j (mm)	2.2±0.97	–	–
SO/O1			
Rz (deg)	6.1±5.10	1.4±0.67	s.e.=0.540, $T_{2,192}$=8.68, P<0.0001
Ry (deg)	2.2±0.97	0.4±0.24	s.e.=0.105, $T_{2,192}$=16.9, P<0.0001
Tx_j (mm)	2.7±2.03	1.0±0.61	s.e.=0.223, $T_{2,192}$=7.65, P<0.0001
FO/O2			
Rz (deg)	13.7±5.29	1.3±0.89	s.e.=0.8564, $T_{2,192}$=22.1, P<0.0001
Ry (deg)	1.9±1.18	0.3±0.21	s.e.=0.126, $T_{2,192}$=12.2, P<0.0001
Tx_j (mm)	3.9±2.35	1.0±0.54	s.e.=0.235, $T_{2,192}$=12.8, P<0.0001
Absolute duration			
Total cycle (ms)	323.7±30.74 (9.50)	281.4±81.82 (29.1)	s.e.=8.04, $T_{2,192}$=5.17, P<0.0001
FC/C (ms)	57.7±17.82 (30.9)	120.4±50.92 (42.3)	s.e.=5.25, $T_{2,192}$=−12.0, P<0.0001
SC (ms)	78.3±25.91 (31.8)	–	–
SO/O1 (ms)	90.6±57.08 (63.0)	97.5±51.76 (53.1)	s.e.=7.73, $T_{2,192}$=−0.930, P=0.354
FO/O2 (ms)	97.1±52.66 (54.2)	65.0±54.22 (83.4)	s.e.=7.74, $T_{2,192}$=4.15, P<0.0001
Relative duration			
FC/C (%)	18.0±5.84 (32.5)	42.9±12.57 (29.3)	s.e.=1.39, $T_{2,192}$=−17.9, P<0.0001
SC (%)	24.1±7.45 (30.9)	–	–
SO/O1 (%)	27.7±16.50 (59.5)	34.5±14.17 (41.2)	s.e.=2.24, $T_{2,192}$=−3.02, P=0.0028
FO/O2 (%)	30.1±16.05 (53.2)	23.1±14.37 (62.1)	s.e.=2.20, $T_{2,192}$=3.205, P=0.0016

Data are means±s.d. with coefficient of variation in parentheses. FC, fast close; SC, slow close; SO, slow open; FO, fast open; C, close, O1, open 1; O2, open 2.

then began to retract (Fig. 3C). During drinking, the anterior tongue marker underwent low amplitude movements, usually outside the oral cavity and occasionally entered it before minimum gape (Fig. 3B). Low amplitude movements were also observed for the posterior tongue marker (Fig. 3D).

We hypothesized that Tx_t displacements of the anterior tongue marker would be larger during drinking, reflecting the tongue's role in fluid ingestion. Contrary to this hypothesis, Tx_t displacements of the anterior tongue marker were significantly larger during chewing than during drinking (Table 2, Fig. 3C,D). However, the overall Tx_t displacement pattern of the posterior marker was more similar between behaviors than that of the anterior marker. Although Tx_t displacements of the anterior tongue marker were significantly smaller during drinking, the anterior tongue marker typically had significantly higher maximum and minimum Tx_t values during drinking versus chewing (Table 2, Fig. 3). These results indicate that the anterior part of the tongue is consistently more protracted during drinking than during chewing, and that it performs greater protraction–retraction movements during chewing. Nevertheless, maximum tongue protraction during chewing was quite variable and contained the drinking maximum and minimum protraction–retraction values within its range. The maximum protracted and retracted values of the posterior tongue marker were not significantly different between behaviors, which likely reflects regional changes in tongue deformation. When Tx_t of the anterior marker was adjusted for displacement from the lower incisor tip (Fig. 4), it was clear that the anterior tongue usually protrudes outside the oral cavity during chewing then retracts into the oral cavity, whereas during drinking, it remains outside the oral cavity and only occasionally retracts back into the oral cavity. Indeed, during chewing, there was usually a single excursion outside the oral cavity during jaw opening whereas during drinking, the tongue was relatively unchanged in its position outside the oral cavity through most of the cycle (Fig. 5).

Timing of tongue protraction–retraction relative to the gape cycle

The timing of maximum and minimum Tx_t of both tongue markers relative to the gape cycle is shown in Fig. 6. During mastication, both markers reached maximum protraction during FO around 75% of the way through the gape cycle, with the anterior marker slightly preceding the posterior one (Fig. 6). During drinking, the anterior marker reached its mean maximum protraction around maximum gape (i.e. at the end of O2) whereas the posterior marker reached its mean maximum protraction earlier during O2 (Fig. 6). However, the overall variance for the timing of maximum marker protraction was high, especially compared with mastication. Only the relative timing of maximum protraction of the anterior marker was statistically different between behaviors, as indicated by the non-overlapping HPDs (Table 3). In contrast, HPDs for the posterior tongue marker overlapped between behaviors, indicating that the null hypothesis of no differences between behaviors cannot be rejected for the posterior region of the tongue. Thus, the protraction of the anterior tongue is delayed, yet more variable, during drinking

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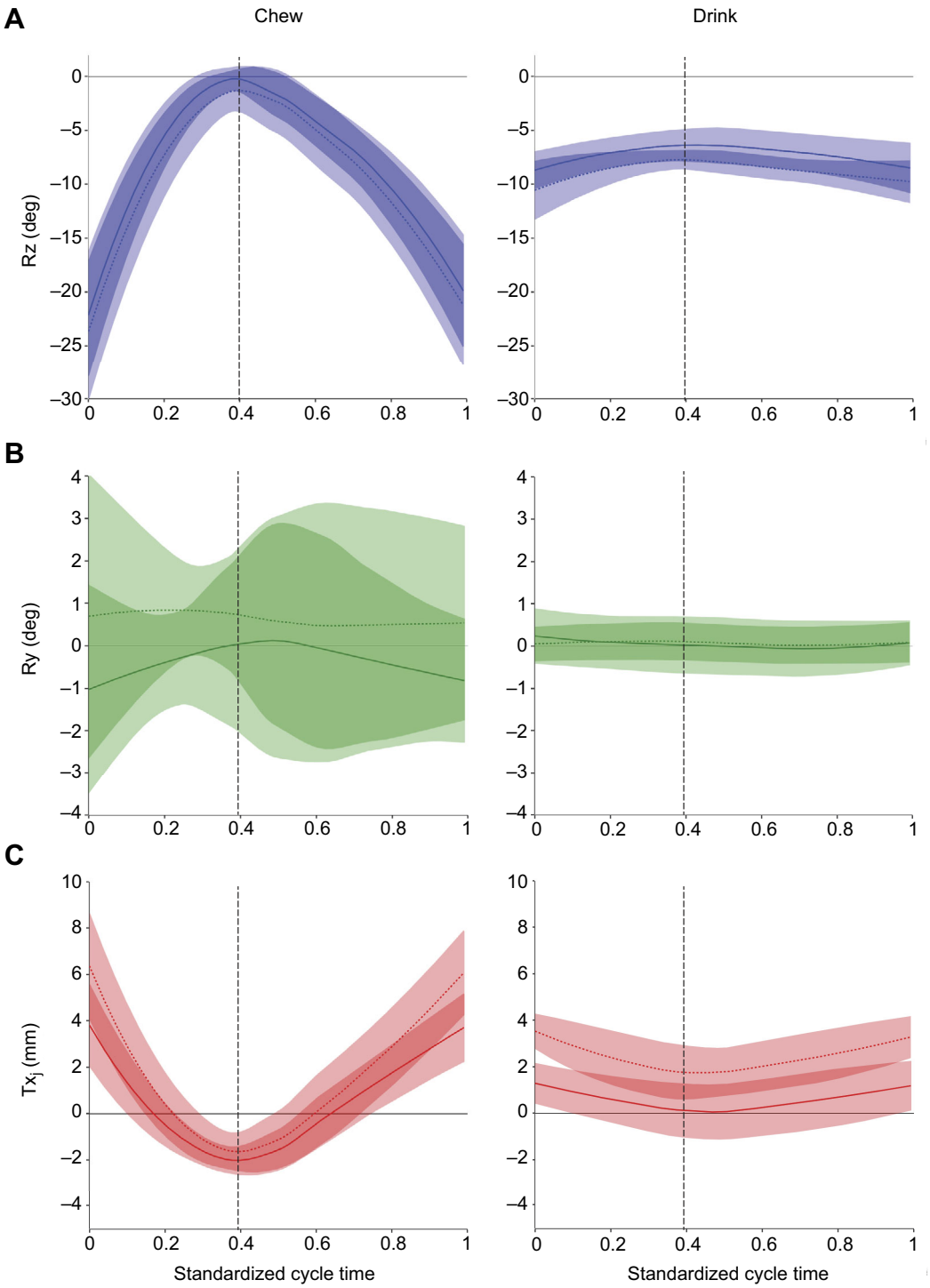

Fig. 2. During drinking, the jaw does not close completely and there is no appreciable yaw. Plots show the mean and 95% confidence intervals (CIs) of Rz, jaw yaw (Ry) and Tx_j repetitive over standardized cycle times for chewing and drinking. Pig ID 20 is represented by solid lines and pig ID 21 is represented by dotted lines. The average time of minimum gape (i.e. maximum Rz) across all cycles is indicated by the vertical dashed line.

versus mastication, whereas the timing of the protraction of the posterior region of the tongue is similar during the two behaviors.

During mastication, the anterior tongue marker usually reached its maximum retracted position (i.e. minimum Tx_t) during FC, whereas the posterior marker reached its maximum retracted position later, usually near minimum gape (Fig. 6). During drinking, both markers were usually fully retracted during closing, with relatively high levels of variance compared with chewing. This higher variance may originate from the relatively flat traces (as illustrated in Fig. 3) because both locators spent a large portion of the cycle at or near their respective maximum retracted position. In spite of this variability, the anterior marker seems to be maximally retracted earlier during chewing than during drinking, whereas the reverse is true for the posterior marker (Fig. 6). However, the HPD intervals for the timing of minimum Tx_t for both markers overlapped between behaviors, indicating no statistical difference (Table 3).

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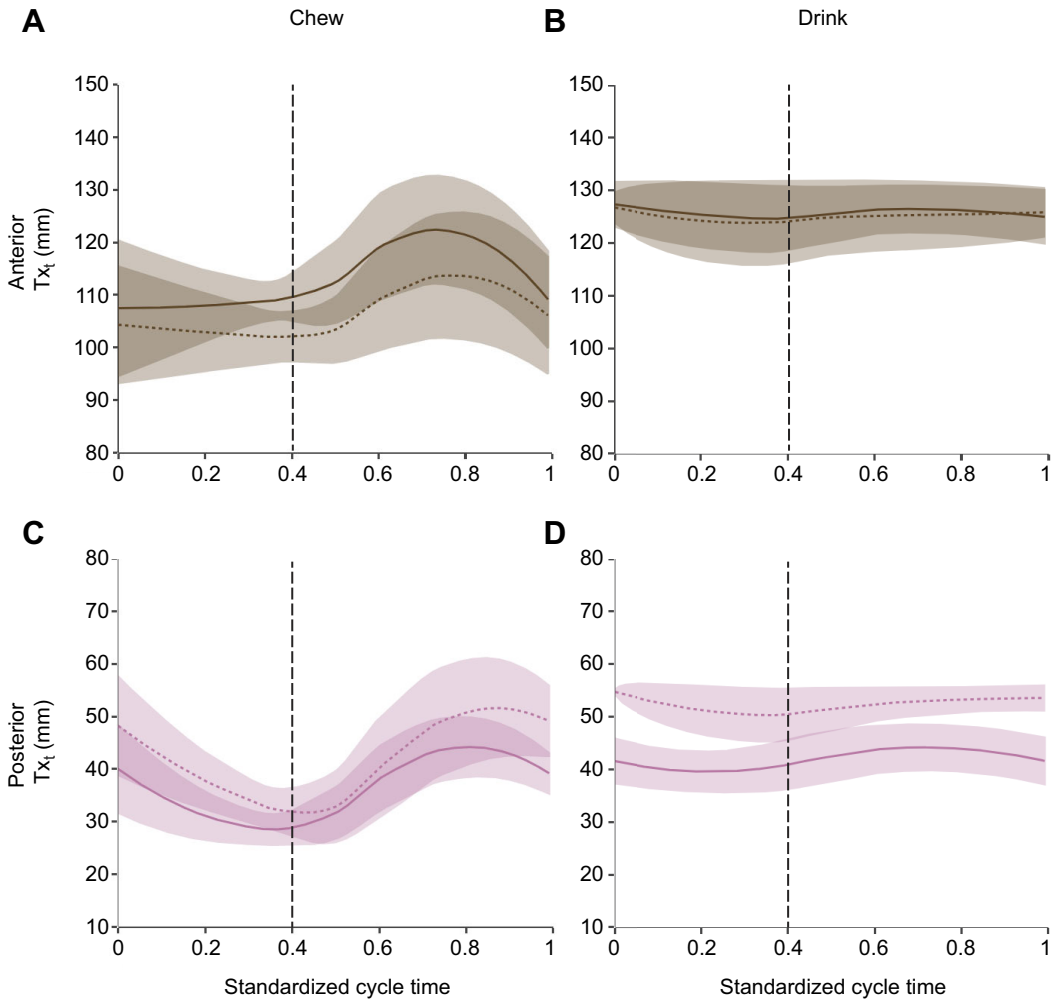

Fig. 3. Both tongue markers undergo a greater range of protraction–retraction during chewing than during drinking. Graphs show the mean lines and their 95% CIs for protraction–retraction (Tx_t) of the anterior (A,B) and posterior (C,D) tongue markers for chewing (left) and drinking (right) plotted against standardized cycle time. Pig ID 20 is indicated by solid lines and pig ID 21 by dashed lines. The dashed vertical line is the mean time of minimum gape.

DISCUSSION

Jaw movements during chewing and drinking

We found that as in chewing, the primary degree of freedom of jaw movements during drinking is Rz (i.e. jaw opening–closing), but the magnitude of pitch change between the two types of cycles was significantly different. Mastication requires food to be positioned and repositioned between the teeth for breakdown, necessitating a larger maximum gape during the chewing cycle. As there is no bolus between the teeth during drinking, only slight jaw opening is necessary for the tongue to protrude and retract to aid in liquid transport into and through the oral cavity (see Movies 1 and 2). This slight jaw opening may also contribute to the fluid acquisition by reducing intraoral pressure, causing water to flow in. For comparison, the mean maximum Rz rotations of the jaw during

Table 2. Anteroposterior translations (Tx_t) of the tongue markers during chewing and drinking and corresponding model results

	Chew	Drink	Model by behavior
Magnitude			
Anterior (mm)	22.5±5.87	6.6±3.56	s.e.=0.684, $T_{2,192}$=23.2, P<0.0001
Posterior (mm)	21.2±4.40	6.7±2.03	s.e.=0.480, $T_{2,192}$=30.4, P<0.0001
Model by marker	s.e.=0.726, $T_{2,192}$=1.73, P=0.0847	s.e.=0.425, $T_{2,192}$=−0.137, P=0.892	
Maximum			
Anterior (mm)	123.4±6.41	128.2±2.29	s.e.=0.554, $T_{2,192}$=−4.64, P<0.0001
Posterior (mm)	50.5±5.02	50.7±4.48	s.e.=0.288, $T_{2,192}$=−1.69, P=0.0927
Model by marker	s.e.=0.806, $T_{2,192}$=90.5, P<0.0001	s.e.=0.450, $T_{2,192}$=172, P<0.0001	
Minimum			
Anterior (mm)	101.0±3.69	121.6±3.49	s.e.=0.492, $T_{2,192}$=−42.0, P<0.0001
Posterior (mm)	29.3±1.71	44.1±5.42	s.e.=0.372, $T_{2,192}$=−39.5, P<0.0001
Model by marker	s.e.=0.398, $T_{2,192}$=180, P<0.0001	s.e.=0.572, $T_{2,192}$=136, P<0.0001	

Data are means±s.d.

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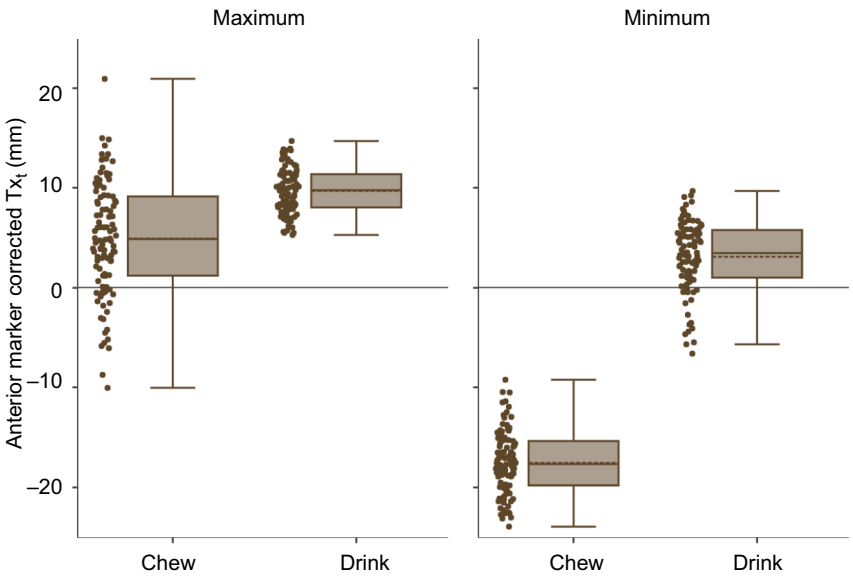

Fig. 4. Corrected maximum Tx$_t$ for the anterior tongue marker. Maximum (left) and minimum (right) Tx$_t$ values for the anterior tongue marker adjusted to incisor location (see Fig. 1), such that positive Tx$_t$ indicates the marker is outside the oral cavity whereas negative Tx$_t$ indicates it is within the oral cavity.

chewing (−21.6 deg) and drinking (−9.6 deg) correspond to approximately 4.3 and 2.0 cm of gape at the incisors, respectively.

At minimum gape, the jaws almost completely closed during chewing cycles, whereas during drinking cycles, the lower jaw was never elevated beyond −5 deg (see Fig. 3A), resulting in a relatively small change in jaw pitch during each cycle (3.17±1.2 deg; Table 1). Lapping in species with incomplete cheeks, such as the cat, demonstrates much larger pitch magnitudes (i.e. over 15 deg in the

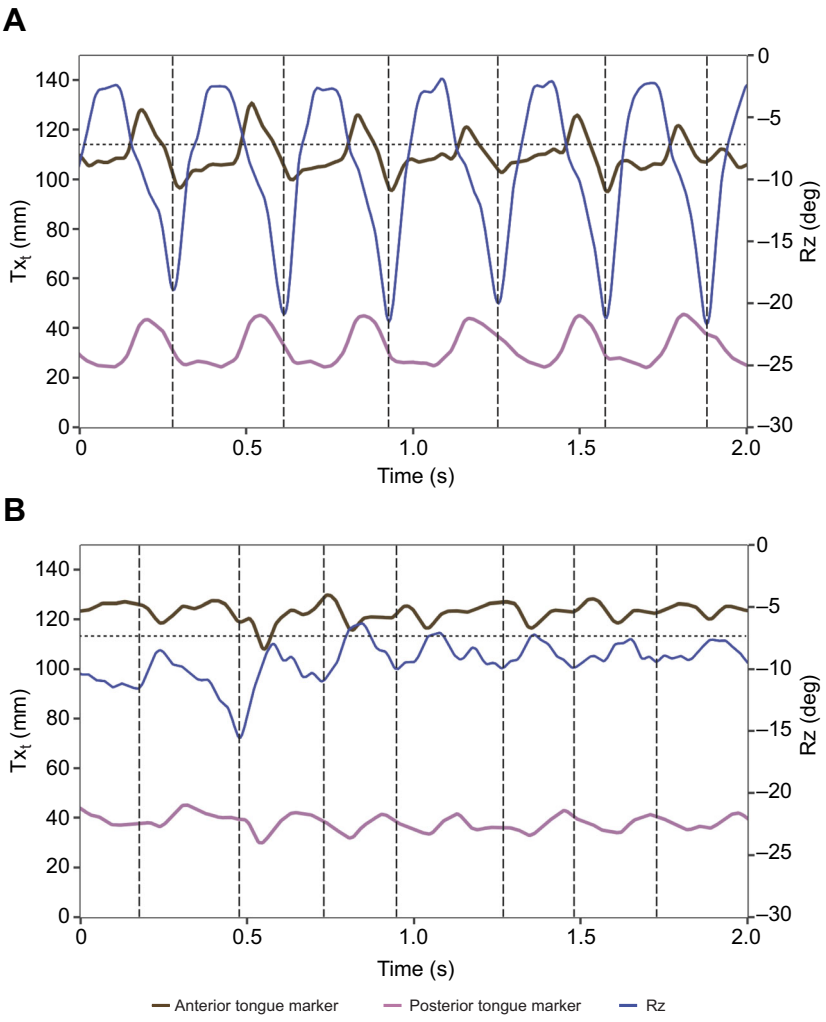

Fig. 5. The anterior and posterior tongue markers are similar in the timing of protraction–retraction within a behavior relative to each other and relative to changes in jaw pitch. Each graph shows representative kinematic profiles of tongue marker protraction–retraction (Tx$_t$) and jaw pitch (Rz) across time during chewing (A) and drinking (B) for pig ID 21. The dotted horizontal line indicates the *x*-coordinate of the incisor tip. Values above this line indicate that the anterior marker is outside the oral cavity whereas values below this line indicate that the anterior marker is within the oral cavity. Vertical dashed lines indicate minimum Rz values, or the transition between cycles.

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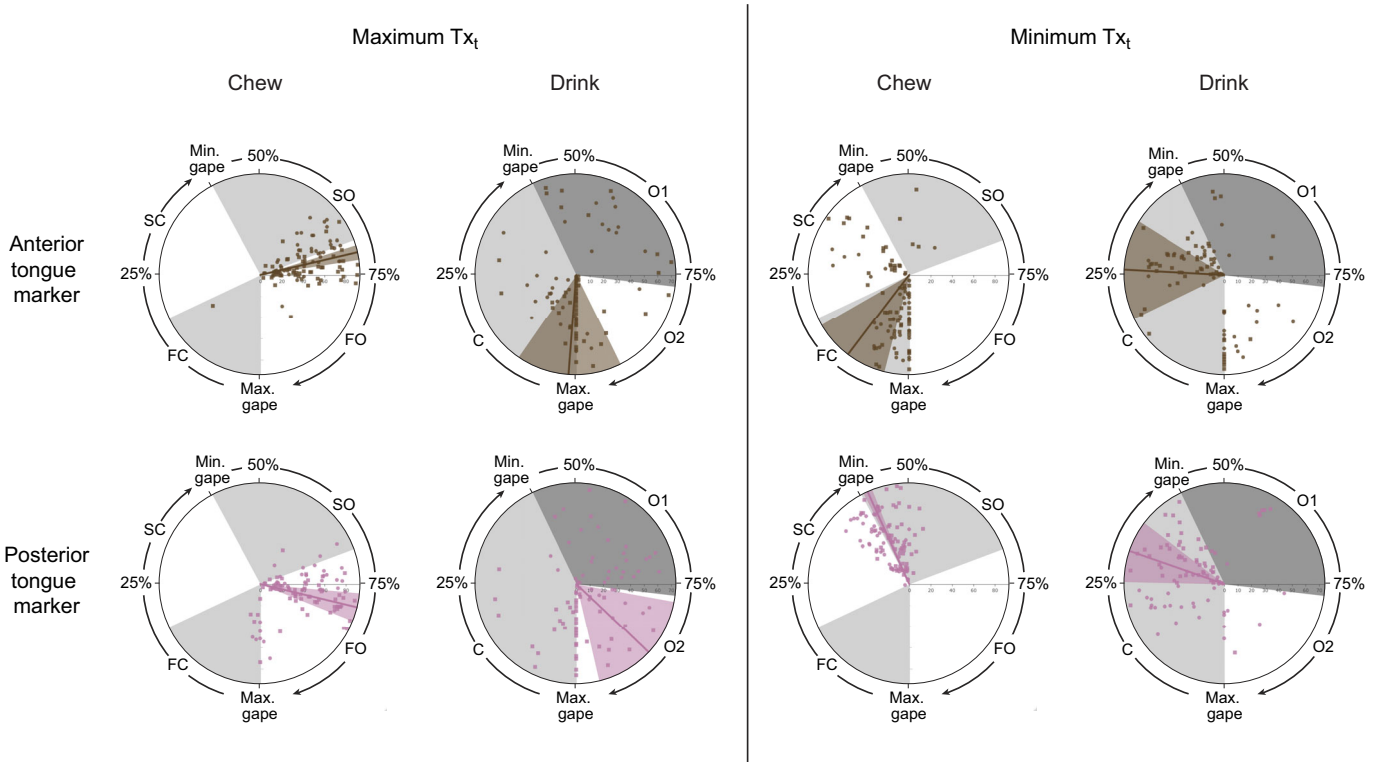

Fig. 6. The timing of maximum Tx$_t$ of the anterior tongue marker is significantly different between chewing and drinking whereas no differences are observed in the timing of the posterior tongue marker. Variance in the timing of maximum and minimum Tx$_t$ is typically higher during drinking than during chewing. In each plot, the timing of maximum (left) or minimum (right) Tx$_t$ for each tongue marker is expressed as a percentage of total cycle duration and shown relative to wedges representing relative mean phase durations (alternating gray and white) during chewing and drinking. Lines indicate mean values and wedges show the corresponding variance (values reported in Table S2). Pig ID 20 is indicated by circles and pig ID 21 by squares. The location on the radius indicates cycle number in the sequence, with more centrifugal points corresponding to cycles later in the sequence.

cat; Hiiemae et al., 1978) than those observed here for drinking. During lapping, the tongue is completely retracted into the oral cavity along with the water as a result of adhesion and inertial mechanisms, and the jaws close to pinch off the liquid column (Crompton and Musinsky, 2011; Reis et al., 2010). In contrast, the low levels of jaw pitch, along with a tongue tip that often does not return to the oral cavity during drinking (Fig. 4) demonstrate that in pigs, sucking is the primary mechanism of liquid transport into the oral cavity, potentially aided by small lapping-like movements of the tongue. The mechanics of sucking in relation to jaw and tongue movements are discussed further below.

The other rotational degree of freedom in jaw movements during chewing cycles is yaw (Ry) to facilitate unilateral food breakdown. Although isognathy in pigs means that both sides occlude during a single cycle (see Herring et al., 2001), there is a clear ‘sidedness’ to the behavior demonstrated by directionality in Ry during SC. This is supported by asymmetrical jaw muscle motor patterns in pigs despite similarities in bone strain patterns on the working (i.e. chewing) and balancing (i.e. non-chewing) sides (Herring, 1976; Herring and Wineski, 1986; Herring et al., 2001). In contrast, during drinking, changes in jaw yaw are virtually absent throughout the entire gape cycle. This confirms that drinking in pigs involves bilaterally symmetrical jaw movements, consistent with our hypothesis. Bilaterally symmetrical jaw movements also occur during infant suckling in the hamster (Lakars and Herring, 1980), during food gathering and the initial cycles of nut crushing in pigs (Menegaz et al., 2015), and they can be inferred for suckling in the pig from their bilaterally symmetrical jaw muscle motor patterns (Herring, 1985b).

Finally, previous work on pigs also shows that of the three available translational DoF, jaw movements during chewing cycles only use anteroposterior (Tx$_j$) translations (Brainerd et al., 2010; Menegaz et al., 2015; Montuelle et al., 2018, 2019, 2020a). We show here that this is also the case for drinking cycles. Moreover, the timing of jaw protraction and retraction is similar between the behaviors as hypothesized: jaw retraction occurs primarily during closing and protraction occurs primarily during opening as was expected. However, the magnitude of Tx$_j$ is much lower during

Table 3. Results of the circular mixed effects model for the timing of maximum and minimum tongue protraction–retraction (Tx$_t$)

	Maximum tongue Tx$_t$ posterior mean (%)		Minimum tongue Tx$_t$ posterior mean (%)	
	Chew	Drink	Chew	Drink
Anterior	71.1±2.66 (65.9, 76.4)	1.7±6.70 (93.9, 14.2)	*8.6±4.46* (*2.5, 16.1*)	*26.4±6.22* (*12.9, 40.0*)
Posterior	*77.5±4.53* (*67.5, 86.8*)	*86.7±10.44* (*55.1, 0.6*)	*43.1±3.43* (*38.7, 46.9*)	*29.2±7.27* (*13.4, 43.9*)

Values are posterior mean±s.d. percentage of standardized cycle time from the Bayesian circular mixed-effects models, with start and end highest posterior density (HPD) intervals in parentheses. Italicized pairs indicate overlapping 95% HPD intervals, supporting the hypothesis of similar timing between behaviors.

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drinking because the jaw is operating over a much narrower range of pitch change. This decreases the translation necessary at the temporomandibular joint (TMJ). As Tx_j still exceeds the precision threshold during drinking, and there is also linear correlation between jaw pitch and protraction–retraction during both behaviors (Fig. 7), this demonstrates basic translational–rotational coupling within the TMJ that is enabled by an expanded articular eminence and relatively open glenoid fossa (Herring and Scapino, 1973; Herring et al., 2002). Condylar translation through jaw opening is hypothesized to decrease masseter and medial pterygoid muscle stretch and preserve muscle torque through large amounts of rotation (Carlson, 1977; Chen, 1998; Hylander, 1978; Smith, 1985). Anteroposterior translation of the jaw may also help to align teeth and aid food breakdown during chewing. During drinking, however, tooth alignment may not be as critical because there is no tooth–food–tooth contact necessary for food breakdown.

Cycle and phase-level durations during chewing and drinking

We initially hypothesized that chewing cycles would be longer and more variable than drinking cycles as a result of the interactions of the teeth and tongue with the food to produce a swallowable bolus. Chewing cycles were on average indeed significantly longer but, contrary to our hypothesis, less variable than drinking cycles. This may be a function of both temporal and spatial factors. Whereas chewing has an SC phase in which jaw closing slows down when the teeth contact the food, this phase was not present in drinking cycles. Rather, there was a single closing phase similar to the FC of chewing in terms of pitch velocity and acceleration. Accordingly, the absolute time spent in jaw closing was longer for chewing (see Table 1). Second, the FO phase was significantly longer during chewing cycles than its opening phase counterpart, O2, during drinking. Finally, the magnitude of jaw opening was larger during chewing and therefore, in the absence of changes in jaw velocity through the cycle, this would extend cycle duration. However, only a weak correlation was observed in the relationship between maximum cycle pitch and cycle duration for both behaviors (Fig. S4). Interestingly, the two behaviors were similar in the relative amount of time spent during jaw closing and jaw opening, although individual relative phase durations differed (see Table 1; Fig. S3).

The differences between chewing and drinking cycle variability are interesting in light of similar analyses from pigs and broader analysis across vertebrates. The results presented here for chewing are comparable to those reported in previous studies on chewing (e.g. Montuelle et al., 2018) and lower than those reported here for drinking. In fact, the comparatively high variability in drinking cycle duration is more consistent with that observed for lepidosaur feeding (Ross et al., 2007a, 2010). It has been hypothesized that protection of the teeth in mammals, rather than energetic savings, facilitates the low CV values observed for cycle duration across mammalian mastication (Ross et al., 2017). As drinking does not have the same constraint relating to tooth protection, there may be fewer constraints for a central control mechanism that maintains high rhythmicity comparable to mastication. Further, the mechanics of fluid transport may also contribute to the variability observed in drinking cycles.

We hypothesized that opening phases would be longer during drinking than during chewing as a result of extraoral excursions of the anterior tongue during these phases. Instead, total closing and total opening durations were similar between behaviors. There were, however, differences in the absolute and relative durations of the opening phases. The first opening phase was longer during drinking than during chewing, and the second opening phase was longer for chewing (both absolute and relative). The relative duration of chewing SO decreases in pigs as food stiffness and toughness increase (Montuelle et al., 2018), such that the relationship observed in this study between chewing and drinking is likely to hold across other foods. Therefore, this long initial opening phase, in which the oral cavity increases in volume, may be functionally relevant to the creation of the pressure gradient necessary for sucking.

We also hypothesized that opening phases would be more variable during chewing than during drinking because of the interactions with the food, which changes properties throughout a sequence. Variability was indeed higher for chewing than for drinking cycles for both absolute and relative duration of the first opening phase, and the opposite was observed for the second opening phase. As occlusion extends into the early stages of the first opening phase (SO; Montuelle et al., 2020a), this higher variability during chewing may be attributed to the changing bolus properties.

Tongue protraction–retraction

Contrary to our hypothesis, the magnitude of anterior tongue protraction and retraction was higher during chewing than during drinking. During most chewing cycles, the anterior tongue marker exited the oral cavity and always retracted more into the oral cavity.

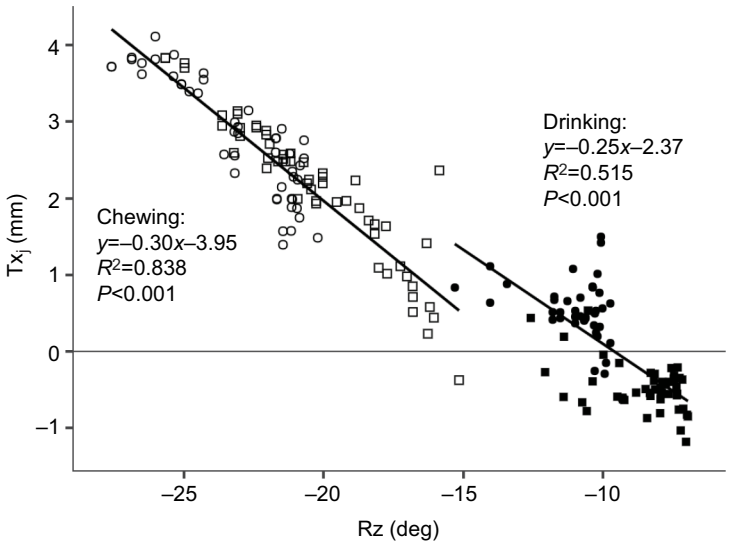

Fig. 7. Jaw protraction–retraction (Tx_j) is significantly negatively correlated with jaw pitch (Rz). Across cycles, larger maximum gape (lower Rz values) corresponds to more jaw protraction (larger Tx_j values) during chewing (open symbols) and drinking (filled symbols). This demonstrates translational–rotational coupling within the temporomandibular joint that is typical of many mammals. Each data point represents jaw Tx_j and its corresponding maximum pitch (i.e. minimum Rz value) for a cycle. Pig ID 20 is represented by circles and pig ID 21 by squares. The least squares linear regression lines, corresponding R^2 and P-values are shown for chewing and drinking cycles.

Maximum protraction during chewing coincided with mid-opening, when the tongue collects the food particles and/or repositions the bolus for the next cycle. During drinking, however, the anterior tongue marker always left the oral cavity but only occasionally retracted fully into it (Fig. 5). This is contrary to lapping in mammals with incomplete cheeks, in which the tongue always retracts fully into the oral cavity in consecutive cycles (Thexton et al., 1998). Whether protraction–retraction movements of the tongue are produced by movements of the tongue base or intrinsic regional deformations, or both, requires further investigation.

When observed without fluoroscopy, pigs appear to use only suction to consume liquids, utilizing low amplitude, rhythmic jaw movements (Herring and Scapino, 1973; Thexton et al., 1998; R.A.O., H.C., S.H.W. and S.J.M., personal observation). However, according to Thexton et al. (1998), pigs utilize a combination of suction and lapping to transport the liquid bolus. The suction component of drinking may be created by the small amounts of jaw opening (i.e. decreasing Rz) that increase the volume of the oral cavity, creating negative pressure within the oral cavity that draws water in. We found that during drinking, the anterior tongue does not undergo significant protraction–retraction, and the timing of its movement is highly variable. This suggests that the anterior tongue plays a minimal role in liquid ingestion. This is in contrast to the pronounced tongue protraction–retraction that occurs during lapping (e.g. Crompton and Musinsky, 2011; Gart et al., 2015). Intrinsic tongue deformations may also contribute to the mechanics of sucking, particularly if shape changes occur in the intraoral region of the tongue. Compared with the significant and rapid oral cavity expansion that occurs during suction feeding for prey capture in aquatic vertebrates, as observed in many fish (e.g. Camp and Brainerd, 2015; Lauder, 1980a,b), the kinematics observed here suggest that pigs require only a small decrease in intraoral pressure for liquid to be drawn into the oral cavity. This is consistent with what has been proposed for the suckling mechanics of infant pigs (Thexton et al., 2004).

Tongue–jaw coordination

We hypothesized that the timing of tongue protraction–retraction would be similar between behaviors, primarily to avoid injury to the tongue. This was observed for the timing of maximum and minimum Tx_t of the posterior tongue marker, albeit with relatively high variability for drinking, and for maximum retraction of the anterior tongue marker (i.e. minimum Tx_t value) during jaw closing. However, the timing of maximum Tx_t of the anterior tongue marker was significantly different between chewing and drinking (i.e. non-overlapping HPDs; Table 3). During chewing, maximum protraction occurred near the transition between SO and FO (75% of total gape cycle duration) with low variance for the anterior tongue marker. During this time, the tongue is collecting and repositioning the food along the tooth row. In contrast, during drinking, maximum protraction of the anterior tongue occurred at maximum gape (100% of total cycle duration, at the O2–C transition), albeit with higher variance. This corresponds to the timing of tongue protraction observed during lapping in the cat (Thexton and McGarrick, 1988). Thus, while there is some variability in protraction timing, the overall pattern is one that is consistent with retracting the tongue as the jaw closes, when there are both functional requirements associated with food or liquid transport as well as protection of the tongue as the teeth approximate. This also likely reflects fundamental properties of the motor control or orofacial movements: coactivation of jaw-opening with tongue-protruding muscles and jaw-closing with tongue-retraction muscles, which is known to occur across a variety of oral behaviors including mastication (e.g. Liu et al., 1993; Naganuma et al., 2001), licking (Travers et al., 1997) and infant suckling (Thexton et al., 1998). The fact that the motoneurons serving the groups of muscles coordinating tongue protrusion with jaw opening as well as tongue retraction with jaw closing share premotor neurons further supports our expectation (Stanek et al., 2014). Nevertheless, the more detailed analysis of these movements here demonstrates anteroposterior variation in tongue protrusion relative to jaw opening, a time when damage is unlikely to occur.

Central control of chewing and drinking behaviors

These differences between drinking and chewing may provide insight into the changes that occur as infants shift from suckling to chewing solid foods and sucking for liquid ingestion. Mammalian infant suckling consists of negative pressure created by suction and/or physical expression of the teat (e.g. Herring, 1985a; Thexton et al., 2004). During both suckling and sucking in pigs, jaw opening appears to be the primary manner in which suction is created. During both behaviors, the tongue is outside the oral cavity for most of the cycle and anteroposterior tongue movements are small, suggesting they contribute little to the creation of suction. As the tongue does not always return to the oral cavity and as the oral opening is continually submerged into the liquid, the small amount of tongue retraction is unlikely to form a liquid column as in lapping. Furthermore, both suckling and drinking appear to be bilaterally symmetrical (Lakars and Herring, 1980), as compared with chewing, which is unilateral, and has clear differentiation of sidedness, in both the jaw and the tongue movements (e.g. Abd-El-Malek, 1955; Hiiemae and Palmer, 2003). Chewing cycles occur at a lower frequency (3.1 versus 3.6 Hz) than drinking cycles, and the frequency of drinking falls within the range of what is observed in infant pig suckling (3.5–4.4 Hz) (German et al., 1997). Therefore, drinking in adult pigs shares some common attributes with infant suckling.

Further investigation into the suckling CPG through the process of weaning would address how these movements are rhythmically controlled and modulated in relation to the development of the masticatory CPG. There is evidence for up to 6 CPGs present during early ontogeny (Barlow, 2009; Nakamura et al., 2004; Tanaka et al., 1999), but how these relate to maturation or shifts in connections between different groups of premotor neurons and/or motoneurons controlling tongue and jaw movements throughout ontogeny is not understood. It appears that there is a shift from a cortical suckling area to a cortical masticatory area across ontogeny in the guinea pig (Iriki et al., 1988), reflecting developmental differences in sensorimotor centers associated with central pattern generation. Suckling rat pups show a motor pattern of nipple attachment that is very similar to that used for chewing whereas the motor pattern for rhythmic suckling from a nipple differs from the chewing motor pattern (Westneat and Hall, 1992). In general, our results suggest that there are connections but also fundamental differences in the central control of sucking and chewing behaviors in pigs.

Conclusions

The 3D kinematics of the jaw and tongue for chewing and drinking in pigs further our understanding of how these movements facilitate different oral behaviors. Compared with chewing, drinking cycles were confirmed to be non-sided and instead only utilize two DoF: jaw pitch and anteroposterior translation. Chewing and drinking cycles were observed to have similar relative contributions of opening and closing to a standardized gape cycle, although with

differing variability for each phase. Differences in tongue protraction–retraction magnitudes were observed, with larger magnitudes of movements observed during chewing. The timing of these movements indicates that some aspects of the tongue–jaw coordination pattern are different between these behaviors. Further, sucking in adults resembles infant suckling, including jaw opening to create suction and the anterior tongue positioned outside the oral cavity. Therefore, drinking cycles show characteristics of both chewing and infant suckling cycles, suggesting further research into the central control of different oral behaviors would provide valuable insight into the development of CPGs across different oral behaviors through ontogeny.

Acknowledgements
The authors would like to thank the Ohio University Laboratory Animal Resources staff for their help with animal husbandry. Dr Andrew Niehaus at The Ohio State University College of Veterinary Medicine and Brooke Keener at the Holzer Clinic assisted with CT scanning of animals. We would also like to thank Volume Graphics GmbH for access to VGSTUDIOMAX 3.3, Marissa O'Callaghan for her assistance with data collection and processing, and Anirudh Ruhil for assistance with data processing. We would also like to thank two anonymous reviewers for their suggestions to improve the manuscript.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: R.A.O., S.J.M., S.H.W.; Methodology: R.A.O., B.A.C.; Software: B.A.C.; Validation: S.J.M., B.A.C.; Formal analysis: R.A.O., H.C.; Investigation: R.A.O., H.C., S.H.W.; Resources: S.H.W.; Data curation: R.A.O., B.A.C., H.C.; Writing - original draft: R.A.O.; Writing - review & editing: R.A.O., S.J.M., B.A.C., S.H.W.; Visualization: R.A.O.; Supervision: S.H.W.; Project administration: S.H.W.; Funding acquisition: R.A.O., S.H.W.

Funding
Funding for this project was provided by grants from the National Institute of Dental and Craniofacial Research (1R15DE023668-01A1), the National Science Foundation (MRI DBI-0922988 and IOS-1456810) and the Ohio Board of Regents to S.H.W., and from the Ohio University Graduate Student Senate, the Ohio University College of Arts and Sciences, the Ohio Center for Ecology and Evolutionary Studies and the Ohio University Student Enhancement Award to R.A.O. Deposited in PMC for release after 12 months.

Data availability
All data used for this study, including metadata, CT scan data and the original unprocessed x-ray movies, have been uploaded to the X-ray Motion Analysis Portal: http://xmaportal.org/webportal/

Supplementary information
Supplementary information available online at
https://jeb.biologists.org/lookup/doi/10.1242/jeb.239509.supplemental

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