Jaw Kinematics and Tongue Protraction-Retraction during Chewing and Drinking in the Pig

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Running title: Pig Tongue Protraction-Retraction

Summary statement: Differences in the magnitude and timing of tongue and jaw movements and the anteroposterior positioning of the tongue during chewing and drinking demonstrate key differences in coordination of these behaviors.

Key Words: tongue, kinematics, XROMM, pig, jaw

Number of Figures: 16

Number of Tables: 5

ABSTRACT

Chewing and drinking are rhythmic and cyclic oral behaviors that require interactions between the tongue, jaw, and a food or liquid bolus, respectively. During chewing, the tongue transports and positions the bolus for breakdown between the teeth. During drinking, the tongue brings the liquid into the mouth during ingestion before transporting it to the oropharynx. The objective of this study is to compare the temporal and spatial dynamics of the jaw during drinking and feeding in pigs and relate these dynamics to protraction-retraction of the tongue. We hypothesize there would be differences in gape cycle dynamics and tongue protraction-retraction between behaviors, reflecting the changing nature of the bolus during chewing. Data were collected from 3-month-old pigs feeding on apples and drinking apple juice. Chewing 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. Drinking jaw movements were of lower magnitude for all degrees of freedom (jaw protraction, yaw, and pitch), with virtually no yaw, and thus were non-sided. The magnitude of tongue protraction-retraction (Tx) was greater during chewing than drinking, but there were minimal differences in the timing of maximum and minimum tongue Tx relative to the jaw gape cycle between behaviors, except for the timing of anterior marker maximum tongue Tx. This suggests there is some variation in tongue-jaw coordination between behaviors. Characterization of jaw and tongue movements for adult chewing and drinking provides insights into differences in the central control of these behaviors.

INTRODUCTION

Feeding and drinking are essential oral behaviors that provide organisms with the necessary nutrients, energy, and hydration for survival. In most mammals, mastication is an important component of feeding that facilitates nutrient and energy acquisition and creates a safely swallowable bolus. Mastication occurs on the postcanine dentition due to the interactions between the occlusal surfaces of opposing upper and lower 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. 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 (Reis et al., 2010; Crompton and Musinsky 2011; Thexton and McGarrick 1988; Thexton and Crompton 1989). 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, chewing 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; Lund and Kolta 2006; Takahashi et al., 2007; Trulsson 2007; Trulsson and Johansson 2002).

Despite extensive modulation of the CPG to adjust for food properties (e.g., Weijs and De Jongh 1977; Dotsch and Dantuma 1989; Davis 2014; Thexton and Crompton 1989; Iriarte-Diaz et al., 2011), gape cycles during chewing are highly rhythmic in mammals (Ross et al., 2007a; 2007b; 2010; 2017). Similar CPGs have been observed for licking, lapping, and sucking behaviors (Nakamura et al., 1999; Barlow 2009; Boughter et al., 2012; Travers et al., 1997), but with contributions from different cortical areas than for mastication (Iriki et al., 1988). Rhythmicity in licking and lapping has been associated with a CPG. In the rat, frequency has been shown to be 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 behavioral shift (Westneat and Hall 1992; German and Crompton 2000; German et al., 2006; German and Crompton 1996), comparatively less is known about the differences and similarities between chewing and adult drinking kinematics and motor control. Limited, research on the cat (Thexton and McGarrick 1988, 1989; Hiiemae et al., 1978) and the opossum (Crompton 1989) has compared jaw and tongue movements during chewing and lapping. Only one study, on pigs, has compared jaw and tongue movements during chewing and sucking but focuses on tongue internal deformations rather than overall movements (Liu et al., 2009).

These studies demonstrate that during chewing, the tongue positions the bolus along the toothrow, usually unilaterally, for processing. When the jaw begins opening, the tongue protrudes to collect the food particles before retracting to reposition the bolus

on the occlusal surface (Crompton 1989; Hiiemae et al., 1978). During lapping, the tongue also protrudes during early opening and then retracts later during opening, trapping the aliquot prior to the next cycle (Hiiemae et al., 1978; Thexton and McGarrick 1988; Crompton 1989; Thexton and Crompton 1989; Reis et al., 2010; Crompton and Musinsky 2011; Gart et al. 2015). During drinking in pigs, the tongue extends into the liquid with the snout immersed, suggesting that the tongue may assist sucking to bring the liquid into the oral cavity (Thexton et al., 1998; German and Crompton 2000), and may potentially be the primary driver of liquid transport (German and Crompton 2000). Thus tongue movements serve distinct functions during chewing and drinking – bolus placement and positioning within the oral cavity during chewing 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 presents study is to compare jaw and tongue kinematics during mastication and drinking in the pig (*Sus scrofa*, Linnaeus 1758) using XROMM with additional soft tissue markers to characterize skeletal and tongue movements, respectively. First, we will determine whether mastication and drinking 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 chewing gape cycles (Montuelle et al., 2020a; Menegaz et al., 2015). Whereas jaw pitch reflects jaw opening and closing, jaw yaw reflects rotation about a vertical axis contributing to the characteristic “sidedness” of

unilateral chewing to facilitate tooth occlusion (see Grossnickle, 2017 and references therein). We hypothesize that chewing and drinking will utilize similar magnitudes of jaw pitch and anteroposterior translation, but jaw yaw will be absent during drinking.

Second, we compare the temporal dynamics of chewing and drinking gape cycles. We hypothesize that chewing cycles will be 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 hypothesize that the jaw opening phases of drinking cycles will be longer than those of chewing cycles due to pronounced extraoral excursions of the anterior tongue during jaw opening.

Finally, we compare protraction and retraction movements of the tongue during feeding and drinking and relate these movements to the temporal dynamics of the gape cycle. We hypothesize that drinking utilizes higher magnitudes of tongue protraction-retraction than chewing in order to ingest and transport liquid to the oropharynx. Because injury to the tongue can occur if these movements are not coordinated (Montuelle et al., 2019; Montuelle et al., 2020b), we hypothesize that the timing of protraction and retraction relative to the gape cycle is similar between the two behaviors and has low variability. Similarity in jaw-tongue coordination between chewing and drinking 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 occurs 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, more detailed analysis of these movements is needed to understand the potential for modification of this coordination across and within behaviors.

By comparing jaw and tongue movements during chewing and drinking, this work will facilitate 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 (orofacial mechanoreceptors) components of the nervous system. Because mammals exhibit two types of rhythmic drinking behaviors throughout their lifespan (i.e., suckling and either lapping, licking, or sucking), any similarities in the kinematics of chewing 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 #s 20 and 21) were quantified using marker-based X-ray Reconstruction of Moving Morphology (XROMM) (Brainerd et al., 2010). In each animal, 5 to 7 1.6 mm diameter radiopaque tantalum markers (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 (1.6 mm diameter) were placed in the tongue, with only the anterior and posterior markers used in this study (see below). After 24-hours of recovery, biplanar

160 fluoroscopy videos were recorded at 250fps using synchronized high-speed digital
161 cameras (Oqus 310, Qualisys, Göteborg, Sweden) while the animals were feeding or
162 drinking. During recording sessions, animals were offered 2cm x 2cm x 1cm cubes of
163 apple or 475 ml of apple juice. Prior to each session, perforated metal sheets (part number
164 9255T641, McMaster-Carr, Robinson, NJ, USA) use for distortion correction and a
165 custom Lego® calibration cube were imaged in each fluoroscopy view to aid in
166 undistorting and calibrating the videos, respectively, following the standard XROMM
167 workflow (Brainerd et al., 2010; Menegaz et al., 2015; Knorlein et al., 2016). Average
168 radiation exposure settings were 100 kVp and 4.3 mA.

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

177 ***XROMM Study and Data Analysis***

178 XMALab (version 1.5.4) was used to perform calibrations, undistort the
179 individual fluoroscopy videos for each sequence, track undistorted marker coordinates in
180 each undistorted and calibrated fluoroscopic view, calculate 3D coordinates of each
181 marker, and reconstruct rigid body transformations, which were filtered using a low-pass
182 Butterworth filter with a cut-off frequency of 25 Hz (Knorlein et al., 2016). In short, the

183 perforated metal sheet was imaged to determine distortions in the field of view whereas
184 the calibration cube was imaged in multiple positions across the field in order to
185 determine the camera position, orientation, and spacing. As this gives orientation and
186 scale to the field of view, marker coordinates can then be translated to calibrated 3D
187 space.

188 A joint coordinate system (JCS) was created in Maya (Autodesk Inc., San Rafael,
189 CA, USA) using the CT reconstruction of the skull and jaw and then used to calculate
190 rotations and translations of the jaw relative to the skull. All axes are perpendicular to
191 each other with the x-axis running anteroposterior in the midline, the y-axis oriented
192 dorsoventrally, and the z-axis oriented along the mediolateral plane running through both
193 condyles (Figure 1A). Both a translation (T) and a rotation (R) is possible about each of
194 these axes, creating a potential for six degrees of freedom (DoF) describing rigid body
195 kinematics: Tx, Ty, Tz, Rx, Ry, Rz.

196 Displacement of the tongue markers were measured relative to a jaw anatomical
197 coordinate system (ACS) (Figure 1B). This system was a more ventrally oriented
198 coordinate system, with the xy- and yz-planes in line with the JCS used to calculate rigid
199 body translations and rotations, but with the xz-plane shifted dorsally so that it is
200 positioned along the hard palate. This allows for the calculation of movements of the
201 anterior and posterior tongue markers (Figure 1C) relative to the jaw while eliminating
202 the influence of gape on translation in the x-dimension (marker Tx: protraction-
203 retraction). Unadjusted tongue marker Tx values (anteroposterior translation: protraction-
204 retraction) indicate displacement from the jaw ACS. Additionally, Tx of the anterior
205 tongue marker was also adjusted so that the tip of the right central incisor defined the

zero-position in the x-dimension (Figure 1C). In this context, positive Tx values indicate the anterior tongue marker being located outside the oral cavity, whereas negative Tx values indicate that it is located within the oral cavity. Note that this is only approximate as the soft tissues surrounding the oral opening (e.g., lips) are not accounted for in the rigid body motion.

After euthanasia, the frozen head of each animal was imaged in motion 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 ± the precision value for each individual determines the threshold for determining jaw movements that exceed error and can be interpreted as real biological motion. Precision thresholds for each animal are provided in Supplemental Table 1.

Waves representing the DoF that exceeded the precision thresholds along with the waves representing tongue protraction-retraction were then analyzed in a custom MATLAB script (FeedCycle: Dr. Brad Chadwell, Idaho College of Osteopathic Medicine) that uses Rz (jaw pitch), the second derivative of Rz (jaw pitch acceleration), and Ry (jaw yaw) to identify key parameters of the gape cycle 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

229 gape) was used to determine the transition from jaw close to jaw open. The maximum
230 negative value (i.e., deceleration) of the second derivative of Rz was then used to divide
231 opening and closing into its constituent phases: fast close (FC), slow close (SC), slow
232 open (SO), and fast open (FO) (Figure 3). The partitioning of gape cycles into phases
233 based on the acceleration of Rz revealed differences between chewing and drinking that
234 impacted subsequent analysis (Figure 3). The four standard phases were observed in
235 chewing cycles (i.e., FC, SC, SO, and FO), whereas only three phases were detected in
236 drinking cycles: one closing phase (C) and 2 opening phases (hereafter called O1 and
237 O2). Because of these differences, we compared drinking and chewing phases
238 corresponding in the directionality (i.e., opening or closing) and acceleration of Rz. Thus,
239 FC of chewing was compared to the single closing phase of drinking, close. For opening,
240 phases were compared based on their order of occurrence, i.e., SO and FO were
241 compared to O1 and O2, respectively, given their presumed functionality in the context
242 of the gape cycle.

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

248 In the chewing dataset used for statistical analysis, we eliminated non-chewing
249 cycles (e.g., ingestion, stage I transport) and dropped all cycles containing a visible
250 swallow. This resulted in 47 chewing cycles and 40 drinking cycles for Pig 20 and 55
251 chewing and 50 drinking cycles for Pig 21. All statistical analyses were performed in R

version 3.6.1 (R core team 2019). On magnitude variables, we used linear mixed effects models with repeated measures, with behavior (chew, drink) as a fixed factor and individual as the random factor using the nlme (*lme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-143) and emmeans (*emmeans: Estimated Marginal Means, aka Least-Squares Means*) packages. Additionally, in order to address variability between chewing and drinking cycle durations, the coefficient of variation (CV) was calculated for each cycle and phase within each sequence. Mean and variance of timing parameters were calculated with the CircStats package (*CircStats*. R package version 0.2-6). For timing parameter models, we used Bayesian circular mixed effects models with repeated measures, with behavior (chew, drink) as a fixed factor and individual as the random factor using the bpnme function (10,000 iterations, 2,000 burn-in, 101 seed, n.lag=3) from the package bpnreg (*bpnreg: Bayseian Projected Normal Regression Models for Circular Data*. R package version 1.0.3) following the methods of Cremers and Klugkist (2018). This method produces the posterior mean, posterior standard deviation, and the 95% highest posterior density interval (HPD). HPDs (Figure 4) are reported as the start position (as % of cycle duration) to end position, where directionality matters. Non-overlapping HPDs indicate a difference between behaviors whereas overlapping HPDs indicate a null hypothesis of no differences between behaviors cannot be rejected.

RESULTS

Jaw Movements and Cycle Dynamics

Jaw movements during rhythmic chewing exceed 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: protraction-retraction) (Figure 2). Ty and Tz occasionally exceed precision thresholds but is of much smaller magnitude than Tx and does not show a rhythmic pattern relative to the gape cycle. Consequently, this likely indicates noise above our precision threshold rather than true movement. In contrast, jaw movements for drinking only exceed precision thresholds for Rz and Tx (Figure 2). Therefore, jaw yaw (Ry) is not a significant movement during drinking, as hypothesized.

The magnitudes of Rz, Ry, and Tx were significantly greater during chewing than during drinking for whole cycles and each intra-cycle phase (Figure 5, Table 1). During both behaviors (Figure 6A), the jaw reaches maximum Rz (i.e., minimum gape) approximately 40% into the cycle. Jaw yaw (Ry) reaches a maximum just after minimum gape during chewing, at which point it resets for the next cycle by switching yaw direction (Figure 6B). In contrast, Ry lacked a discernible peak during drinking, further supporting that it is bilaterally symmetrical behavior, unlike chewing. For both behaviors, jaw retraction (i.e., decreasing Tx) occurs during jaw closing whereas protraction (i.e., increasing Tx) occurs during opening (Figure 6C).

Absolute total cycle and phase durations are shown in Figure 7A, whereas their descriptive statistics and the results of the linear mixed effects models are reported in Table 2. Chewing cycles were significantly longer than drinking cycles. Comparison of

phases reveals that the absolute duration of C during drinking was significantly longer than the corresponding FC of chewing. Contrary to our hypothesis for jaw opening, SO and O1 absolute duration did not differ between the two behaviors, but FO was significantly longer than O2. The average coefficient of variation (CV) of chewing cycle duration across all sequences (9.50) was lower than for drinking cycle duration (29.1). At the phase level, no clear patterns were observed in variability between chewing and drinking cycles, contrary to our hypothesis. Overall, more variation was observed for opening phases of both chewing and drinking cycles than for the closing phases (Table 2).

The relative contribution of each phase to total gape cycle duration also differed between the two behaviors (Figure 7B). Whereas C and O1 are 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 (Figure 8). Higher variability was also observed for opening phases of both chewing and drinking cycles relative to closing phases (Table 2).

Tongue Protraction-Retraction

Anteroposterior tongue marker displacements (Tx), reflecting tongue protraction-retraction, relative to the gape cycle during representative chewing and drinking cycles are shown in Figure 9. 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. For most of the chewing cycle, the anterior marker is located within the oral cavity during chewing, with usually a single excursion outside the oral cavity (Figure 9A) whereas during drinking, it is usually outside the oral cavity and may occasionally enter it

before minimum gape (Figure 9B). During chewing, the anterior marker protracts during opening (Figure 10A) whereas during drinking only small displacements are observed (Figure 10B). The posterior marker retracts during closing for chewing cycles, reaches a minimum near minimum gape, and then reaches maximum protraction during opening, before it then begins to retract (Figure 10C). During drinking, Tx magnitudes are lower for both markers, and the tongue is almost always in a protracted position compared to resting position (Figure 10C,D).

Contrary to the hypothesis, Tx displacements of the anterior tongue marker are significantly higher during chewing than during drinking (Table 3; Figure 11). However, the anterior tongue marker also typically has significantly higher maximum and minimum Tx values during drinking than chewing (Figure 12; Table 4). These results indicate that the anterior part of the tongue is consistently more protracted during drinking than during chewing, but that it performs greater protraction-retraction movements during chewing. Nevertheless, maximum tongue protraction during chewing is quite variable and contains the drinking maximum and minimum protraction-retraction values within its range (Figure 12A). The maximum protracted and retracted values of the posterior tongue marker are not significantly different between behaviors (Table 4). However, during chewing the posterior marker retracts more than during drinking. When Tx of the anterior marker is adjusted for displacement from the lower incisor tip (Figure 13), it is 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. Whether this is

contributed to movements at the tongue base or intrinsic deformations, or both, requires further investigation.

Timing of Tongue Protraction-Retraction Relative to the Gape Cycle

The timing of maximum and minimum Tx of both tongue markers relative to the gape cycle are shown in Figure 14. Timing and variance values are reported in Supplemental Table 2. During chewing, both markers reach maximum protraction during FO around 75% of the way through the gape cycle, with the anterior marker slightly preceding the posterior (Figure 14). During drinking, the anterior marker reaches its mean maximum protraction around maximum gape (i.e., at the end of O2) whereas the posterior marker reaches its mean maximum protraction earlier during O2 (Figure 14). However, the overall variance for the timing of maximum marker protraction is high, especially compared to chewing. The relative timing of maximum protraction of only the anterior marker is statistically different for chewing and drinking as indicated by the non-overlapping HPDs (Table 5). In contrast, HPDs for the posterior tongue marker overlap indicating that the null hypotheses of no differences between behaviors cannot be rejected. Thus, the protraction of the anterior tongue is delayed, yet more variable, during drinking compared to chewing, whereas the timing of the protraction of the posterior region of the tongue is similar in both behaviors.

During chewing, the anterior tongue marker usually reaches its maximum retracted position (i.e., minimum Tx) during FC, whereas the posterior marker reaches its maximum retracted position near minimum gape (Figure 14). During drinking, both markers are usually fully retracted during closing, with relatively high levels of variance compared to chewing. This higher variance during drinking may originate from the

relatively flat traces (as illustrated in Figure 10), because both locators spend a large portion of the cycle at or near their respective maximum retracted position. The anterior marker is maximally retracted earlier during chewing than during drinking, whereas the reverse is true for the posterior marker (Figure 14). However, the HPD intervals for the timing of minimum Tx for both markers overlap between chewing and drinking, indicating no statistical difference between behaviors (Table 5).

DISCUSSION

Jaw Movements during Chewing and Drinking

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 between chewing and drinking is significantly different. Chewing 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. For comparison, the mean maximum Rz rotations of the jaw during chewing (-21.6°) and drinking (-9.6°) correspond to approximately 4.3 cm and 2.0 cm of gape at the incisors, respectively.

At minimum gape, the jaws almost completely close during chewing, whereas during drinking, the lower jaw never elevates beyond -5° (see Figure 6A) resulting in a relatively small change in jaw pitch during each cycle (3.17° ± 1.2; Table 1). Lapping in species with incomplete cheeks, such as the cat, demonstrate much larger pitch magnitudes (i.e., over 15° in the 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 due to adhesion and inertial mechanisms, and the jaws close to pinch off the liquid column (Reis et al., 2010; Crompton and Musinsky 2011). In contrast, the low levels of jaw pitch in pigs, along with a tongue tip that often does not return to the oral cavity during drinking (Figure 13) demonstrate that in pigs, sucking is the primary mechanism of liquid transport into the oral cavity, aided by small lapping 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 is yaw (Ry) to facilitate unilateral chewing. Although isognathy in pigs means that both sides occlude (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 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 only use anteroposterior (Tx) 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. 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 is much lower during 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 still exceeds the precision threshold during drinking, and there is also linear correlation between jaw pitch and protraction-retraction during both behaviors (Figure 15), this demonstrates the basic translational-rotational anatomical coupling mechanism within the TMJ that is typical of many mammals. The functional significance of this mechanism is still debated, but one likely hypothesis is that it maximizes the mechanical advantage of the masseter throughout changes in jaw pitch (Hylander 1992; Chen 1998; 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 cycle durations would be similar between chewing and drinking cycles, but that chewing will be more variable due to the interactions of the teeth and tongue with the food to produce a swallowable bolus. Contrary to this hypothesis, chewing cycles were on average significantly longer and less variable than drinking cycles. Longer chewing cycles may be a function of both temporal and spatial factors. First, 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, which have 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 2). Second, the FO phase was significantly longer than its opening phase counterpart, O2, during drinking. Finally, the magnitude of jaw opening was larger during chewing and therefore, absent changes in jaw velocity through the cycle, this would extend cycle duration. If this is the case, we would expect a linear relationship in which an increase in cycle pitch magnitude is correlated with an increase in cycle duration. However, when the relationship between pitch magnitude and cycle duration is examined (Figure 16), it is apparent that there are differences in the average velocity of jaw pitch between behaviors. Interestingly, both behaviors were similar in the relative amount of time spent during jaw closing and during jaw opening, although individual relative phase durations differed (see Table 2; Figure 8).

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

less selection for a central control mechanism that maintains high rhythmicity comparable to mastication.

We hypothesized that opening phases will be longer during drinking than chewing, correlating with the extraoral excursions of the anterior tongue during these phases. Instead, total close and total open 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 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. Additionally, we hypothesized that opening phases would show higher variability during chewing than drinking because of the interactions with the food, which changes properties throughout a sequence. Variability was indeed higher for chewing than 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 first opening phase (Montuelle et al., 2020a), this higher variability during chewing may be attributed to the changing bolus properties.

Tongue Protraction-Retraction and Tongue-Jaw Coordination

Contrary to our hypothesis, the magnitude of protraction and retraction (Tx) of the anterior tongue marker is higher during chewing compared to drinking (Figure 11). These movements are influenced by movements of the hyoid combined with intrinsic

deformations of the tongue. During most chewing cycles, the anterior tongue marker exited the oral cavity and always retracted more into the oral cavity. During drinking, however, the anterior tongue marker always leaves the oral cavity but only occasionally retracts fully into it (Figure 13). This is contrary to lapping in mammals with incomplete cheeks, in which the tongue always retracts into the oral cavity in successive cycles (Thexton et al., 1998).

When observed without fluoroscopy, pigs appear to use suction to consume liquids, utilizing low amplitude, rhythmic jaw movements (Herring and Scapino 1973; Thexton et al., 1998; pers. obs.). 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 and creating a negative pressure within the oral cavity that draws water in. Intrinsic tongue deformations may also contribute to the mechanics of sucking. Compared to 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., Lauder 1980a; 1980b; Camp and Brainerd 2015), liquid ingestion using suction in mammals may only need a small pressure gradient for liquid to be drawn into the oral cavity, similar to the suckling mechanism of infant pigs (Thexton et al., 2004).

As tongue-jaw coordination is important for preventing injury to the tongue, we hypothesized that the timing of protraction-retraction would be similar between behaviors. This is observed for the timing of maximum and minimum Tx of the posterior tongue marker, which is not significantly different between behaviors (Figure 14), albeit

with relatively high variability for drinking. However, the timing of maximum Tx of the anterior tongue marker is significantly different between chewing and drinking (i.e., non-overlapping HPDs; Table 5). During chewing, maximum protraction occurs 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 occurs at maximum gape (100% of total cycle duration, at the O2-closing transition), although with higher variance. This corresponds to the timing of tongue protraction observed during lapping in the cat (Thexton and McGarrick 1988). There was no difference between behaviors when the anterior tongue marker reaches its maximum retracted position (i.e., minimum Tx value) during jaw closing. These tongue movements are coupled with hyoid and jaw movements, in addition to intrinsic deformations (Hiiemae and Palmer 2003).

Central Control of Chewing and Drinking Behaviors

Insights into the similarities and differences between drinking and chewing may provide insight into the relationship between infant suckling and the shift to chewing and drinking. In opossums, the introduction of small food particles into the oral cavity while drinking induces a jaw opening reflex, like that observed during chewing (Thexton and Crompton 1989), indicating peripheral components of the nervous system may influence processing of a solid versus liquid bolus. As mammals mature, they transition from suckling to more complex jaw movements underlying mastication as well as other methods of liquid ingestion (e.g., sucking, lapping). Mammalian infant suckling may consist of negative pressure and/or physical expression of the teat (e.g., Herring 1985a;

524 Thexton et. al., 2004). As the main mechanism of suction is the creation of a pressure
525 gradient, jaw opening is the primary driver of these cycles. This functionally shifts a SC-
526 dominated power stroke during chewing to an opening-phase power stroke during
527 drinking (Barlow 2009). We observed a similar trend here, where liquid transport is
528 dominated by tongue movements during the open phases of the gape cycle. Furthermore,
529 both suckling and drinking appear to be bilaterally symmetrical (Lakars and Herring
530 1980), as compared to chewing which is unilateral, and has clear differentiation of
531 sidedness, both of the jaws and the tongue (e.g., Abd-El-Malek 1955; Hiiemae and
532 Palmer 2003). Chewing cycles occur at a lower frequency (3.1 vs 3.6 Hz) than drinking,
533 and the frequency of drinking falls within the range of what is observed in infant pig
534 suckling (3.5-4.4 Hz) (German et al., 1997). Therefore, drinking in adult pigs shares
535 some common attributes with both infant suckling and adult masticatory movements.
536 Further investigation into the suckling CPG through the process of weaning
537 would address how these movements are rhythmically controlled and modulated in
538 relation to the development of the masticatory CPG. There is evidence for up to 6 CPGs
539 present during early ontogeny (Barlow 2009; Tanaka et al., 1999; Nakamura et al., 2004),
540 but how these relate to maturation or shifts in connections between different groups of
541 premotor neurons and/or motoneurons controlling tongue and jaw movements throughout
542 ontogeny is not understood. It appears that there is a shift from a cortical suckling area to
543 a cortical masticatory area across ontogeny in the guinea pig (Iriki et al., 1988), reflecting
544 developmental differences in sensorimotor centers associated with central pattern
545 generation. Suckling rat pups show a motor pattern of nipple attachment that is very
546 similar to that used for chewing and is suggested to be homologous to chewing, but the

motor pattern for rhythmic suckling from a nipple differs from the chewing motor pattern (Westneat and Hall 1992). Our results suggest that there are connections between but also fundamental differences in the central control of sucking and chewing behaviors.

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. 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 observed during chewing. The timing of these movements indicates that some aspects of the tongue-jaw coordination pattern is different between these behaviors. 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.

ACKNOWLEDGMENTS

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 and Marissa O'Callaghan for her assistance with data collection and processing.

COMPETING INTERESTS

No competing interests declared.

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 SHW 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 RAO.

DATA AVAILABILITY

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

TABLES

Table 1. Maximum cycle and phase magnitudes for Rx, Ry, and Tx of the jaw with corresponding model results

Phase	Behavior	Rz (deg) Mean ± SD	Rz Model	Ry (deg) Mean ± SD	Ry Model	Tx (mm) Mean ± SD	Tx Model
Total Cycle	Chew	20.8 ± 2.4	SE = 0.276 $T_{2,192} = 64.2$ $p < 0.0001$	3.66 ± 0.79	SE = 0.0859 $T_{2,192} = 34.3$ $p < 0.0001$	6.98 ± 1.3	SE = 0.117 $T_{2,192} = 42.0$ $p < 0.0001$
	Drink	3.17 ± 1.2		0.708 ± 0.26		2.08 ± 0.41	
Fast Close / Close	Chew	13.7 ± 3.3	SE = 0.365 $T_{2,192} = 29.6$ $p < 0.0001$	1.32 ± 0.52	SE = 0.0609 $T_{2,192} = 11.4$ $p < 0.0001$	4.29 ± 1.6	SE = 0.159 $T_{2,192} = 15.3$ $p < 0.0001$
	Drink	2.90 ± 1.2		0.625 ± 0.28		1.87 ± 0.59	
Slow Close	Chew	6.32 ± 2.7	—	1.15 ± 0.79	—	2.25 ± 0.97	—
	Drink	—		—		—	
Slow Open / Open 1	Chew	6.12 ± 5.1	SE = 0.540 $T_{2,192} = 8.68$ $p < 0.0001$	2.20 ± 0.97	SE = 0.105 $T_{2,192} = 16.9$ $p < 0.0001$	2.68 ± 2.0	SE = 0.223 $T_{2,192} = 7.65$ $p < 0.0001$
	Drink	1.43 ± 0.67		0.431 ± 0.24		0.976 ± 0.61	
Fast Open / Open 2	Chew	13.7 ± 5.3	SE = 0.8564 $T_{2,192} = 22.1$ $p < 0.0001$	1.89 ± 1.2	SE = 0.126 $T_{2,192} = 12.2$ $p < 0.0001$	3.95 ± 2.3	SE = 0.235 $T_{2,192} = 12.8$ $p < 0.0001$
	Drink	1.29 ± 0.89		0.345 ± 0.21		0.963 ± 0.54	

Table 2. Absolute and relative cycle and phase durations with corresponding model results

	Absolute Durations			**Relative Durations (% Cycle Duration)**		
Phase	**Chew Mean ± SD (CV)**	**Drink Mean ± SD (CV)**	**Model**	**Chew Mean ± SD (CV)**	**Drink Mean ± SD (CV)**	**Model**
Total Cycle	323 ± 31 (9.50)	281 ± 82 (29.1)	SE = 8.04 $T_{2,192} = 5.17$ $p < 0.0001$	—	—	—
Fast Close / Close	57.7 ± 18 (30.9)	120 ± 51 (42.3)	SE = 5.25 $T_{2,192} = -12.0$ $p < 0.0001$	18.0 ± 5.8 (32.5)	42.9 ± 13 (29.3)	SE = 1.39 $T_{2,192} = -17.9$ $p < 0.0001$
Slow Close	78.3 ± 25 (31.8)	—	—	24.1 ± 7.4 (30.9)	—	—
Slow Open / Open 1	90.6 ± 57 (63.0)	97.5 ± 52 (53.1)	SE = 7.73 $T_{2,192} = -0.930$ $p = 0.354$	27.7 ± 17 (59.5)	34.5 ± 14 (41.2)	SE = 2.24 $T_{2,192} = -3.02$ $p = 0.0028$
Fast Open / Open	97.1 ± 53 (54.2)	65.0 ± 54 (83.4)	SE = 7.74 $T_{2,192} = 4.15$ $p < 0.0001$	30.1 ± 16 (53.2)	23.1 ± 14 (62.1)	SE = 2.20 $T_{2,192} = 3.205$ $p = 0.0016$

Table 3. Magnitude of tongue Tx with corresponding model results

	Chew Cycles Mean (mm) ± SD (CV)	**Drink Cycles Mean (mm) ± SD (CV)**	**Model by Marker**
Anterior	22.5 ± 5.9	6.60 ± 3.6	SE = 0.684 $T_{2,192} = 23.2$ $p < 0.0001$
Posterior	21.2 ± 4.4	6.65 ± 2.0	SE = 0.480 $T_{2,192} = 30.4$ $p < 0.0001$
Model by Behavior	SE = 0.726 $T_{2,192} = 1.73$ $p = 0.0847$	SE = 0.425 $T_{2,192} = -0.137$ $p = 0.892$	

Table 4. Value of tongue Tx relative to the jaw coordinate system

	Maximum Tx (mm)			**Minimum Tx (mm)**		
	Chew Cycles	**Drink Cycles**	**Model by Behavior**	**Chew Cycles**	**Drink Cycles**	**Model by Behavior**
Anterior	123 ± 6.4	128 ± 2.3	SE = 0.554 $T_{2,192} = -4.64$ $p < 0.0001$	101 ± 3.7	122 ± 3.5	SE = 0.492 $T_{2,192} = -42.0$ $p < 0.0001$
Posterior	50.5 ± 5.0	50.7 ± 4.5	SE = 0.288 $T_{2,192} = -1.69$ $p = 0.0927$	29.3 ± 1.7	44.1 ± 5.4	SE = 0.372 $T_{2,192} = -39.5$ $p < 0.0001$
Model by Marker	SE = 0.806 $T_{2,192} = 90.5$ $p < 0.0001$	SE = 0.450 $T_{2,192} = 172$ $p < 0.0001$		SE = 0.398 $T_{2,192} = 180$ $p < 0.0001$	SE = 0.572 $T_{2,192} = 136$ $p < 0.0001$	

Table 5. Results of the circular mixed effects model for the timing of maximum tongue Tx

	Posterior Mean ± sd **(start, end)**		**Posterior Mean** ± sd **(start, end)**	
	Chew Cycles	**Drink Cycles**	**Chew Cycles**	**Drink Cycles**
Anterior	71.1 ± 2.7 (65.9, 76.4)	1.7 ± 6.7 (93.9, 14.2)	8.6 ± 4.5 (2.5, 16.1)	26.4 ± 6.2 (12.9, 40.0)
Posterior	77.5 ± 4.5 (67.5, 86.8)	86.7 ± 10.4 (55.1, 0.6)	43.1 ± 3.4 (38.7, 46.9)	29.2 ± 7.2 (13.4, 43.9)

Values are reported as a percentage of standardized cycle time.

FIGURE LEGENDS

Figure 1. Jaw and tongue coordinate systems and tongue marker locations. (A) Orientation of the temporomandibular joint coordinate system for characterizing jaw movement, (B) orientation of the anatomical coordinate system relative to the jaw used for characterizing tongue protraction-retraction (i.e., tongue Tx) , and (C) locations of the anterior (brown) and posterior (pink) tongue markers relative to the jaw at rest. Adjusted Tx values for the anterior tongue marker are corrected relative to the tip of the right lower incisor (orange X). Positive Tx indicates the anterior marker is outside the oral cavity and negative Tx indicates that the marker is inside the oral cavity. The posterior tongue marker Tx is in reference to the zero position of the jaw anatomical coordinate system shown in (B).

Figure 2. Graphs of the 6 DoF during 1.6 seconds of feeding (left) and drinking (right) from Individual 21. Translations are shown on the top and rotations are on the bottom. Shaded area represents the precision threshold about the sequence mean. * next to each shaded area indicates the DoF exceeds the precision thresholds.

Figure 3. Graph of jaw pitch (Rz, blue) and acceleration (grey) during a representative chewing and drinking cycles from Individual 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.

Figure 4. Schematic demonstrating interpretation of 95% highest posterior density intervals (HPDs). (A) An HPD of (25.0, 75.0), shown by the shaded area, indicates there is a 95% probability that the posterior mean is contained within this range. (B) An HPD of (75.0, 25.0) includes the cycle start, as indicated by the shaded region, as the start HPD position is higher than the end HPD position. Non-overlapping HPDs indicate a difference between behaviors whereas overlapping HPDs indicate a null hypothesis cannot be rejected. (A) and (C) have overlapping HPDs (from 25-35% of cycle duration), and therefore are not statistically different as the null hypothesis cannot be rejected. The same is true for (B) and (C) as they also have overlapping HPDs (from 15-25% of cycle duration). (B) and (D) also overlap. Because the HPD for (D) is contained within (B), they are not statistically different. (A) and (D), and (C) and (D) do not have overlapping HPDs, and therefore have significantly different means.

Figure 5. The magnitudes of jaw Rz, Ty, and Tx are greater during chewing than during drinking. Magnitude of (A) jaw pitch - Rz, (B) jaw yaw - Ry, and (C) anteroposterior translation - Tx for total cycle and constituent phases for chewing (grey) and drinking (white). The box represents the first and third quartiles, and the mean and median are indicated by the dashed and solid lines, respectively. Whiskers represent the upper and lower fence (±1.5 interquartile range). Individual values are shown to the left of each box. Chewing phases are: FC, fast close; SC, slow close; SO, slow open; and FO, fast open. Drinking phases are: C, close; O1, open 1; and O2, open 2.

Figure 6. During drinking, the jaw does not reach closure and there is no appreciable yaw. Plots shows the mean and 95% confidence intervals of Rz, Ry and Tx and their 95% confidence intervals over standardized cycle times for chewing and drinking. Individual 20 is represented by solid lines and Individual 21 is represented by dashed lines. The average time of minimum gape (i.e., maximum Rz) across all cycles is indicated by the vertical dashed line.

Figure 7. Chewing cycles are significantly longer than drinking cycles. The absolute duration of C during drinking is significantly longer than the corresponding FC of chewing. SO and O1 absolute duration does not differ between the two behaviors, but FO was significantly longer than O2. Chewing is represented by grey boxes and drinking by white. Total cycle and absolute phase durations are shown in A. Relative phase durations (as percent of total cycle duration) are shown in B. Boxplot characteristics are described in Figure 5. Chewing phases are: FC, fast close; SC, slow close; SO, slow open; and FO, fast open. Drinking phases are: C, close; O1, open 1; and O2, open 2.

Figure 8. Both behaviors have a similar proportion of opening and closing phases. However, FO contributes more to total cycle duration for chewing cycles than O2 does for drinking cycles. Mean phase duration as a percentage of standardized gape cycle are shown for chewing (left) and drinking (right). Each wedge represents the proportion of mean total gape cycle duration for each phase. Chewing phases are: FC, fast close; SC, slow close; SO, slow open; and FO, fast open. Drinking phases are: C, close; O1, open 1; and O2, open 2.

Figure 9. 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) relative to jaw pitch during 3 sequential cycles of chewing (A) and drinking (B) for Individual 21. The dotted horizontal line indicates the location 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 maximum Rz values, or the transition between cycles.

Figure 10. Both tongue markers undergo a greater range of protraction-retraction during chewing than during drinking. Graphs show the mean lines and their 95% confidence intervals for protraction-retraction of the anterior (A, B) and posterior (C, D) tongue markers for chewing (left), and drinking (right) plotted against standardized to cycle time. Individual 20 is indicated by solid lines and Individual 21 by dashed lines. The dashed vertical lines is the mean time of minimum gape.

Figure 11. Higher magnitudes of Tx are observed for both tongue markers during chewing. Boxplot characteristics are described in Figure 5.

Figure 12. The tongue performs greater protraction-retraction movements during chewing. Graphs show the maximum (left) and minimum (right) Tx for anterior (A) and posterior (B) tongue markers during chewing and drinking. Values indicate Tx relative to the jaw coordinate system. Boxplot characteristics are described in Figure 5.

Figure 13. Corrected maximum Tx for the anterior tongue marker. Maximum (left) and minimum (right) Tx values for the anterior tongue marker adjusted to incisor location (see Figure 1), such that +Tx indicates the marker is outside the oral cavity whereas -Tx indicates it is within the oral cavity.

Figure 14. The timing of maximum Tx 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 tongue Tx is typically higher during drinking than chewing. In each plot, the timing of maximum (left) or minimum (right) Tx for each tongue marker is expressed as a percent 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 Supplemental Table 2). Individual 20 is indicated by circles and Individual 21 by squares. The horizontal bar indicates cycle number of the cycle from the sequence.

Figure 15. Jaw protraction-retraction (Tx) is strongly correlated with jaw pitch (Rz). This demonstrates the basic translational-rotational anatomical coupling mechanism within the TMJ that is typical of many mammals. Each datapoint represents jaw Tx and its corresponding maximum pitch (i.e., minimum Rz value) for a cycle. Chewing cycles are indicated by open symbols and drinking by solid symbols. Individual 20 is represented by circles and Individual 21 by squares. The least squares linear regression line and corresponding R^2 is shown for combined chewing and drinking cycles.

Figure 16. The average velocity of jaw pitch differs between chewing and drinking. Each datapoint represents the cycle duration and the corresponding maximum pitch (i.e., minimum Rz value) for a cycle. The least squares linear regression line and corresponding R^2 are shown for chewing cycles (open markers) and drinking cycles (solid markers). Individual 20 is represented by circles and Individual 21 by squares.

Figure 1

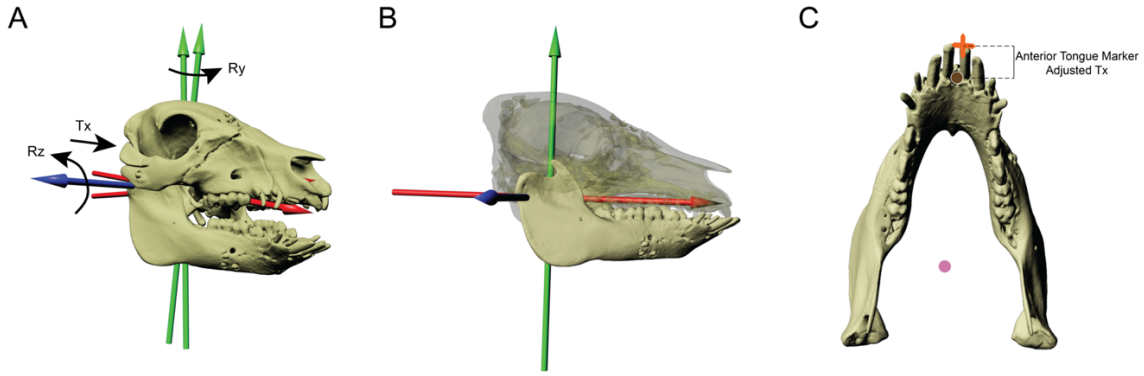


Figure 2

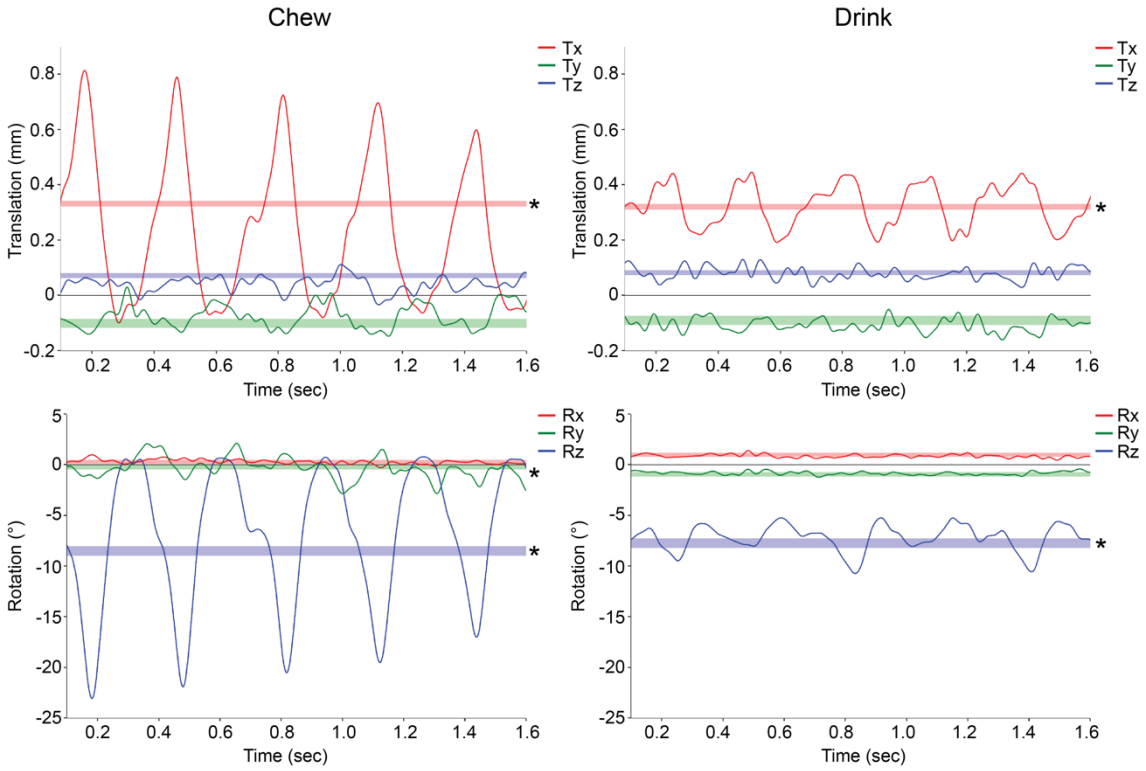


Figure 3

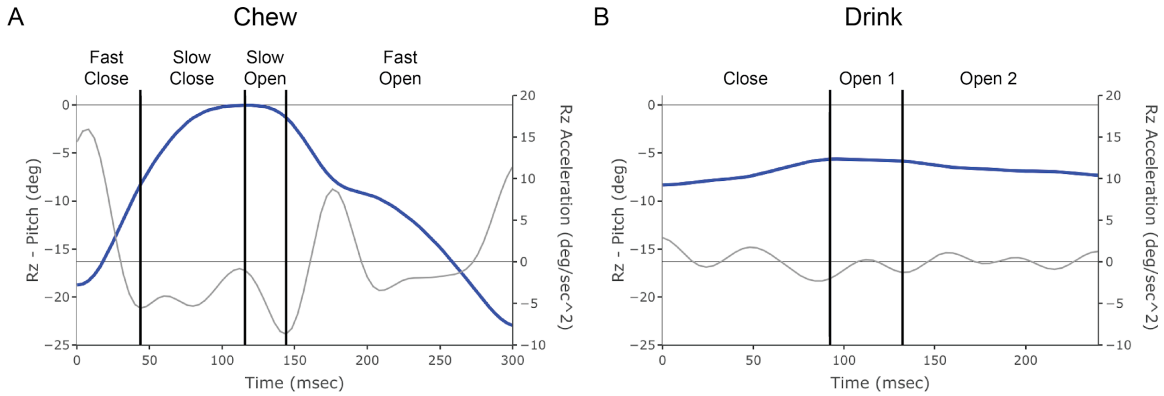

A
Chew
Fast Close
Slow Close
Slow Open
Fast Open
Rz - Pitch (deg)
Rz Acceleration (deg/sec^2)
Time (msec)
B
Drink
Close
Open 1
Open 2
Rz - Pitch (deg)
Rz Acceleration (deg/sec^2)
Time (msec)

Figure 4

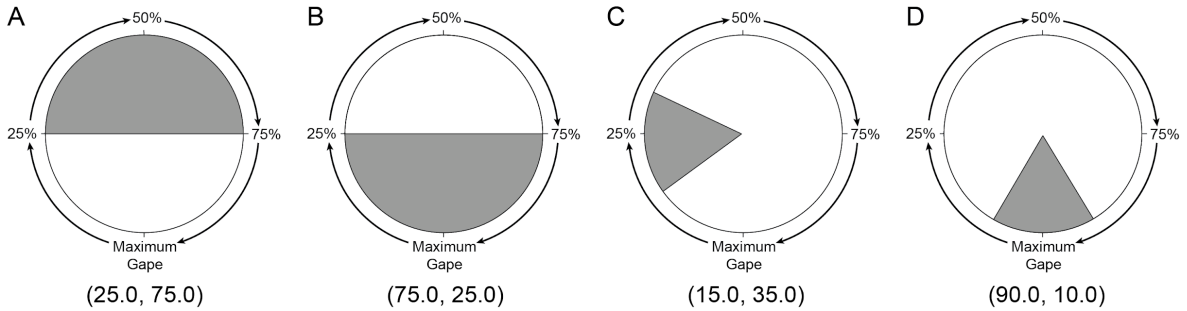

A
50%
25%
75%
Maximum
Gape
(25.0, 75.0)
B
50%
25%
75%
Maximum
Gape
(75.0, 25.0)
C
50%
25%
75%
Maximum
Gape
(15.0, 35.0)
D
50%
25%
75%
Maximum
Gape
(90.0, 10.0)

Figure 5

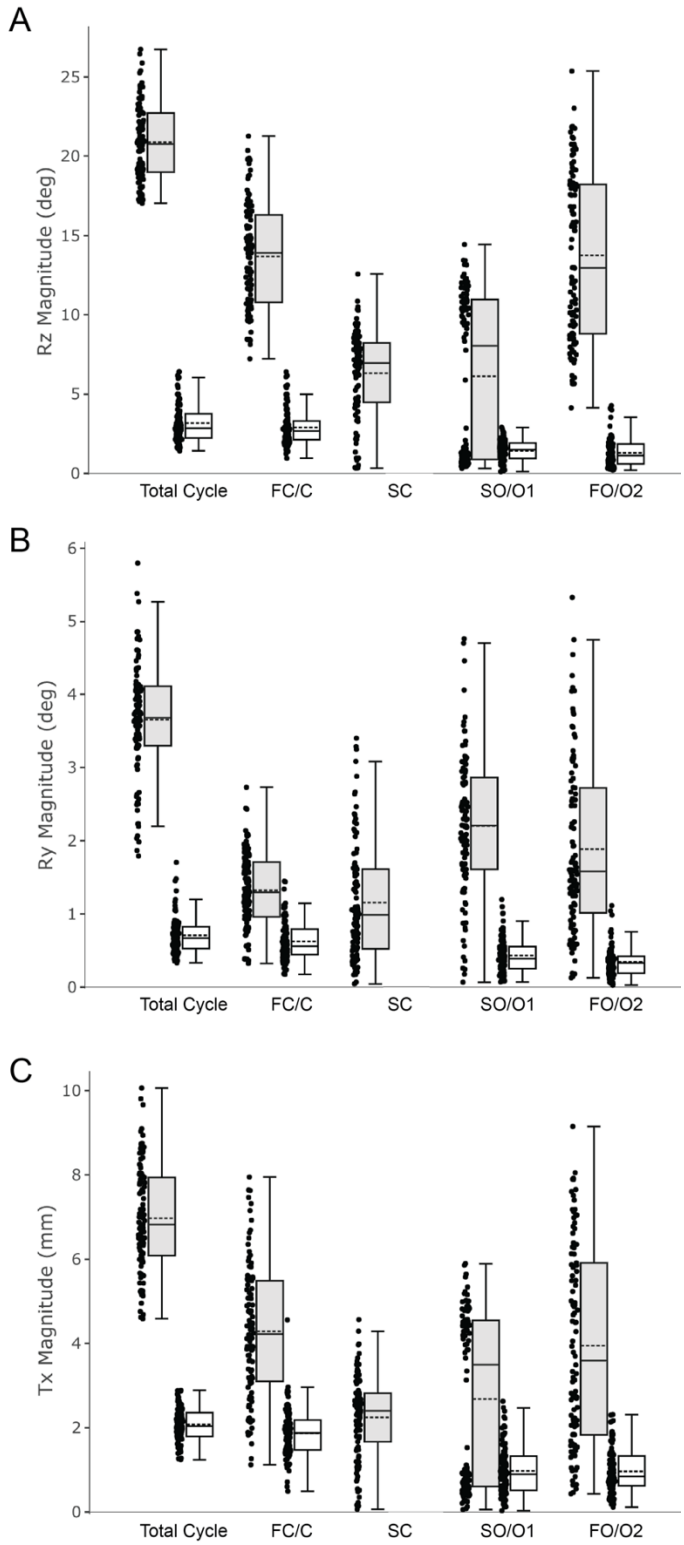

A
Rz Magnitude (deg)
0
5
10
15
20
25
Total Cycle
FC/C
SC
SO/O1
FO/O2
B
Ry Magnitude (deg)
0
1
2
3
4
5
6
Total Cycle
FC/C
SC
SO/O1
FO/O2
C
Tx Magnitude (mm)
0
2
4
6
8
10
Total Cycle
FC/C
SC
SO/O1
FO/O2

Figure 6

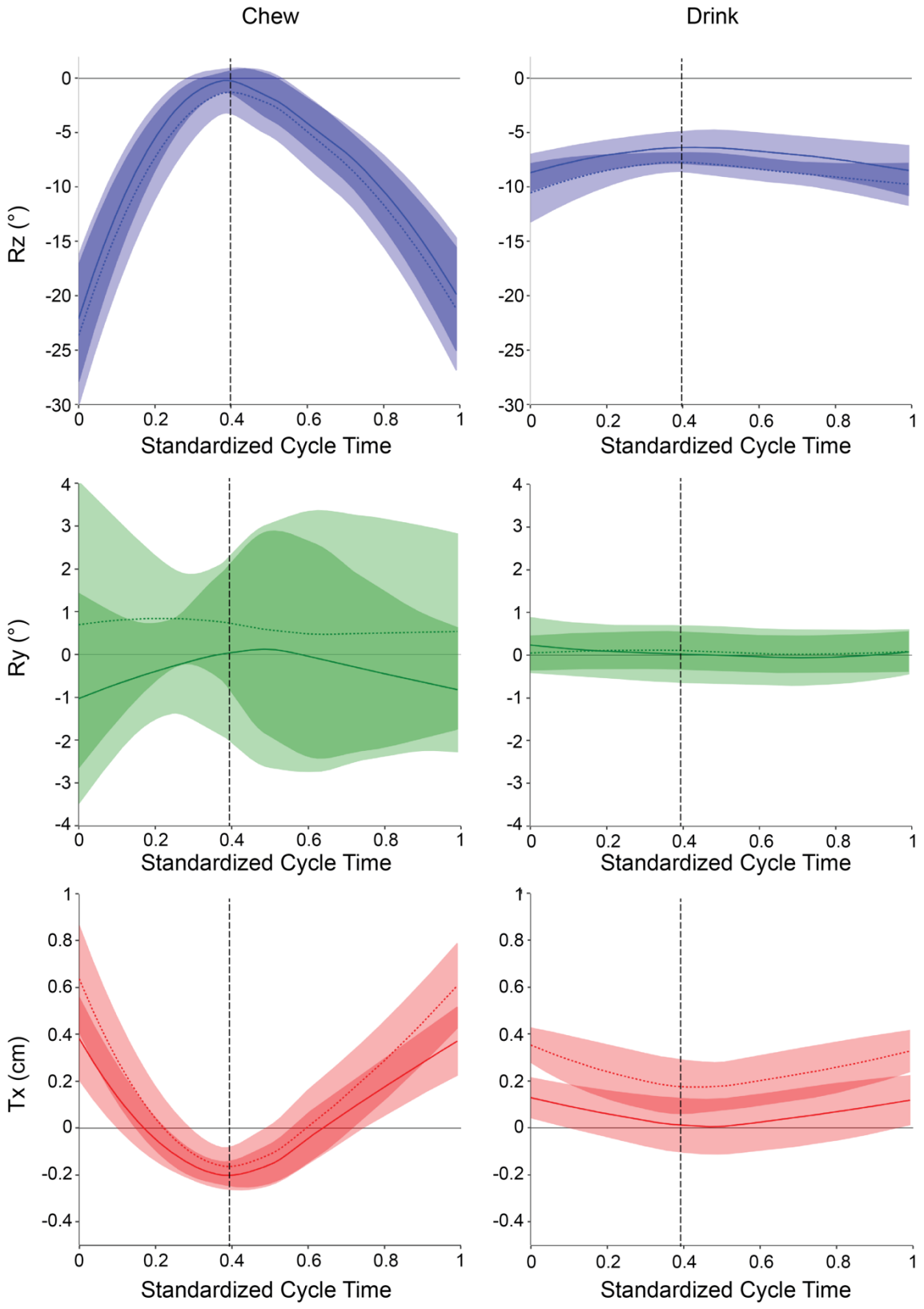
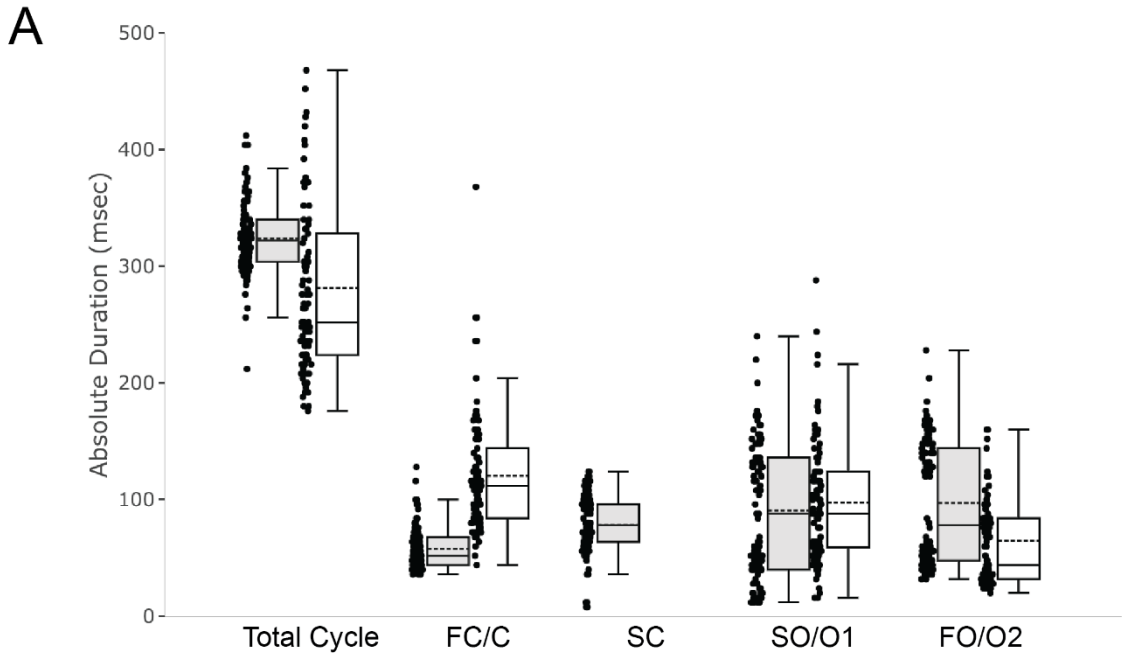


Figure 7


A
Absolute Duration (msec)
500
400
300
200
100
0
Total Cycle
FC/C
SC
SO/O1
FO/O2

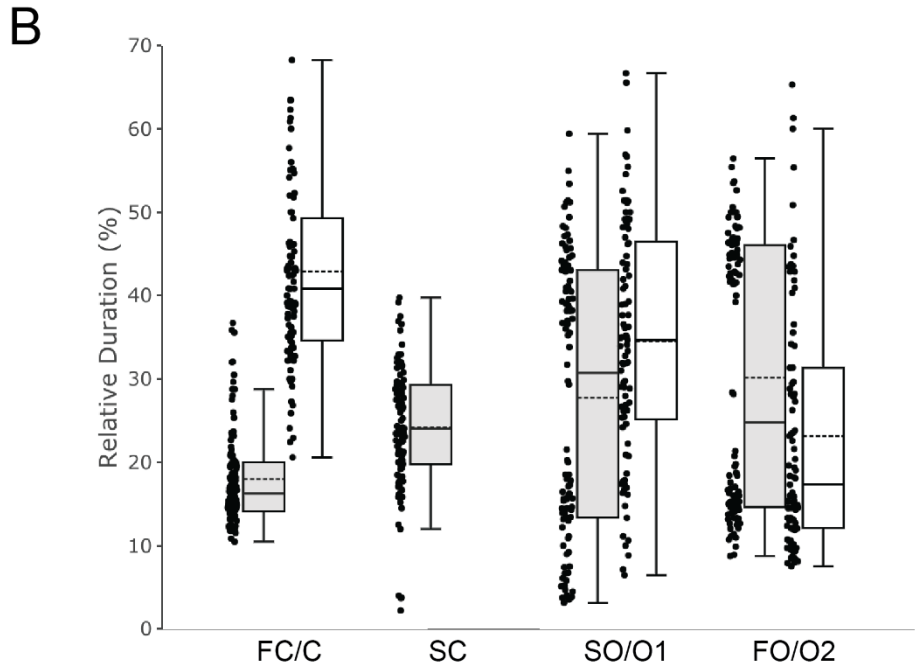

B
Relative Duration (%)
70
60
50
40
30
20
10
0
FC/C
SC
SO/O1
FO/O2

Figure 8

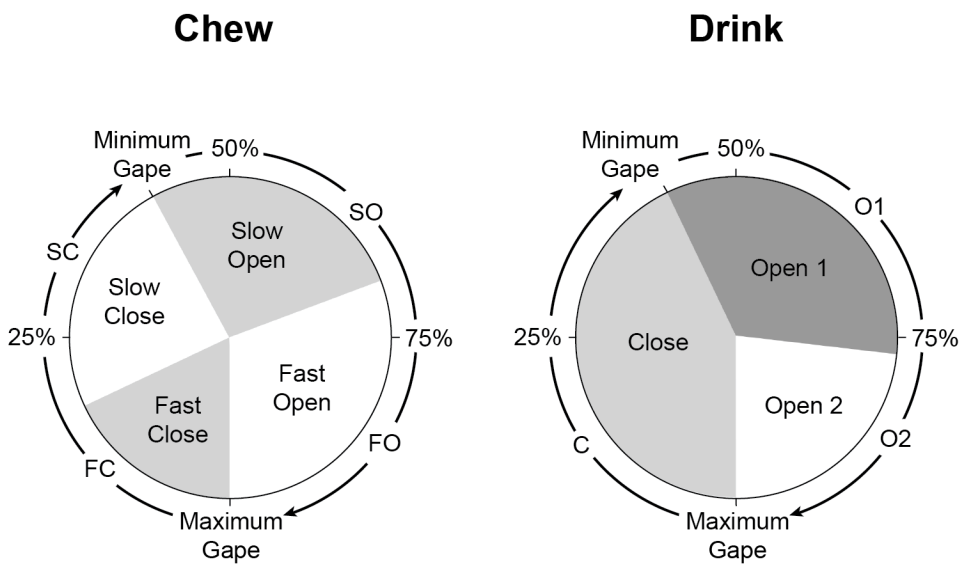

Chew
Minimum Gape
50%
SO
Slow Open
SC
Slow Close
25%
75%
Fast Open
Fast Close
FO
FC
Maximum Gape
Drink
Minimum Gape
50%
O1
Open 1
25%
Close
75%
Open 2
C
O2
Maximum Gape

Figure 9

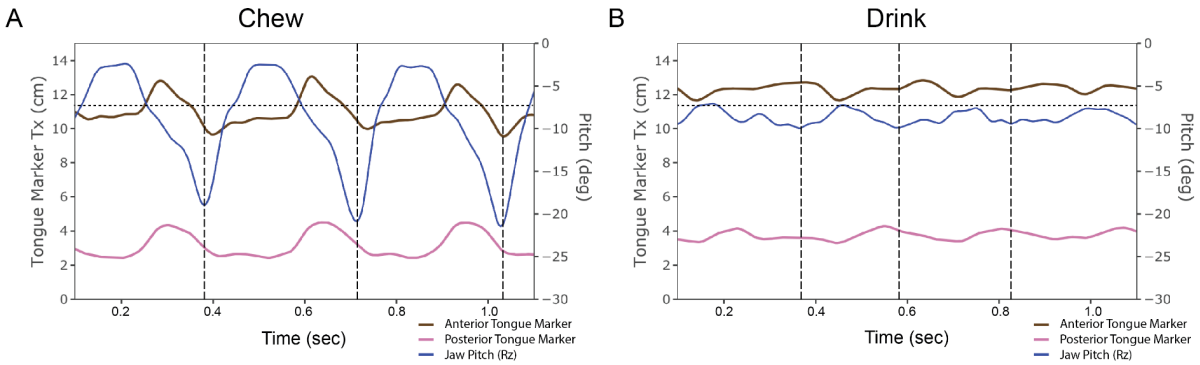

A
Chew
B
Drink
Tongue Marker Tx (cm)
Pitch (deg)
Time (sec)
Anterior Tongue Marker
Posterior Tongue Marker
Jaw Pitch (Rz)

Figure 10

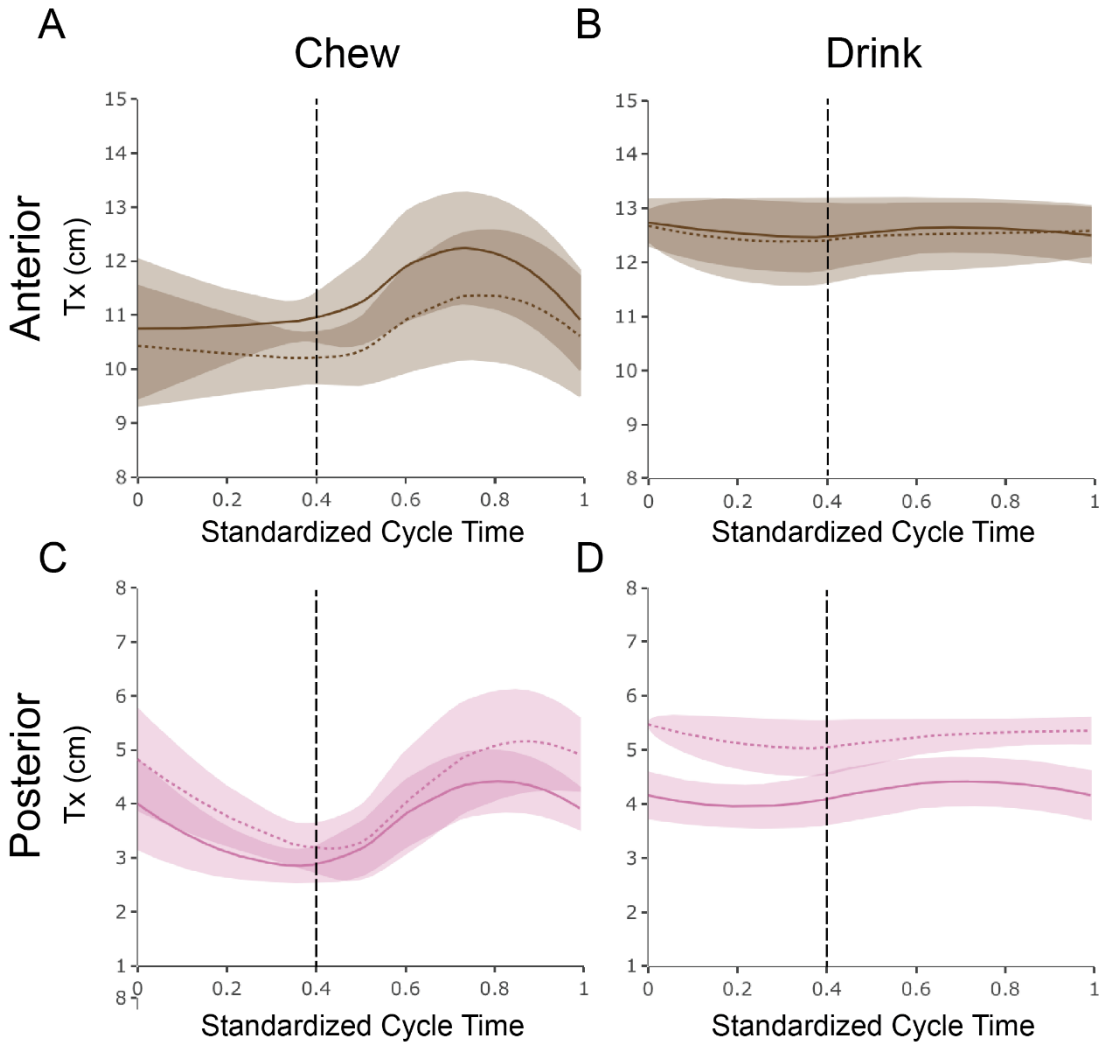

A
Chew
B
Drink
Anterior
Tx (cm)
15
14
13
12
11
10
9
8
0
0.2
0.4
0.6
0.8
1
Standardized Cycle Time
C
D
Posterior
Tx (cm)
8
7
6
5
4
3
2
1
Standardized Cycle Time

Figure 11

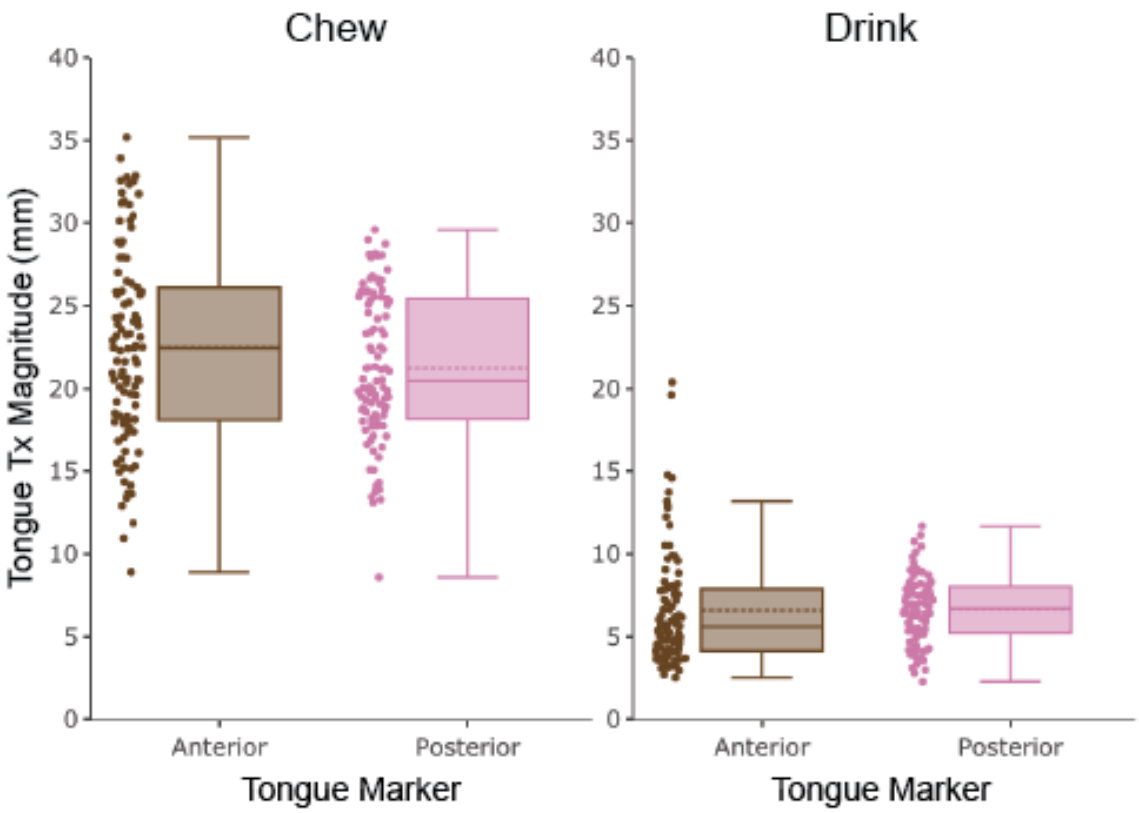

Chew
Drink
Tongue Tx Magnitude (mm)
40
35
30
25
20
15
10
5
0
Anterior
Posterior
Tongue Marker
Anterior
Posterior
Tongue Marker

Figure 12

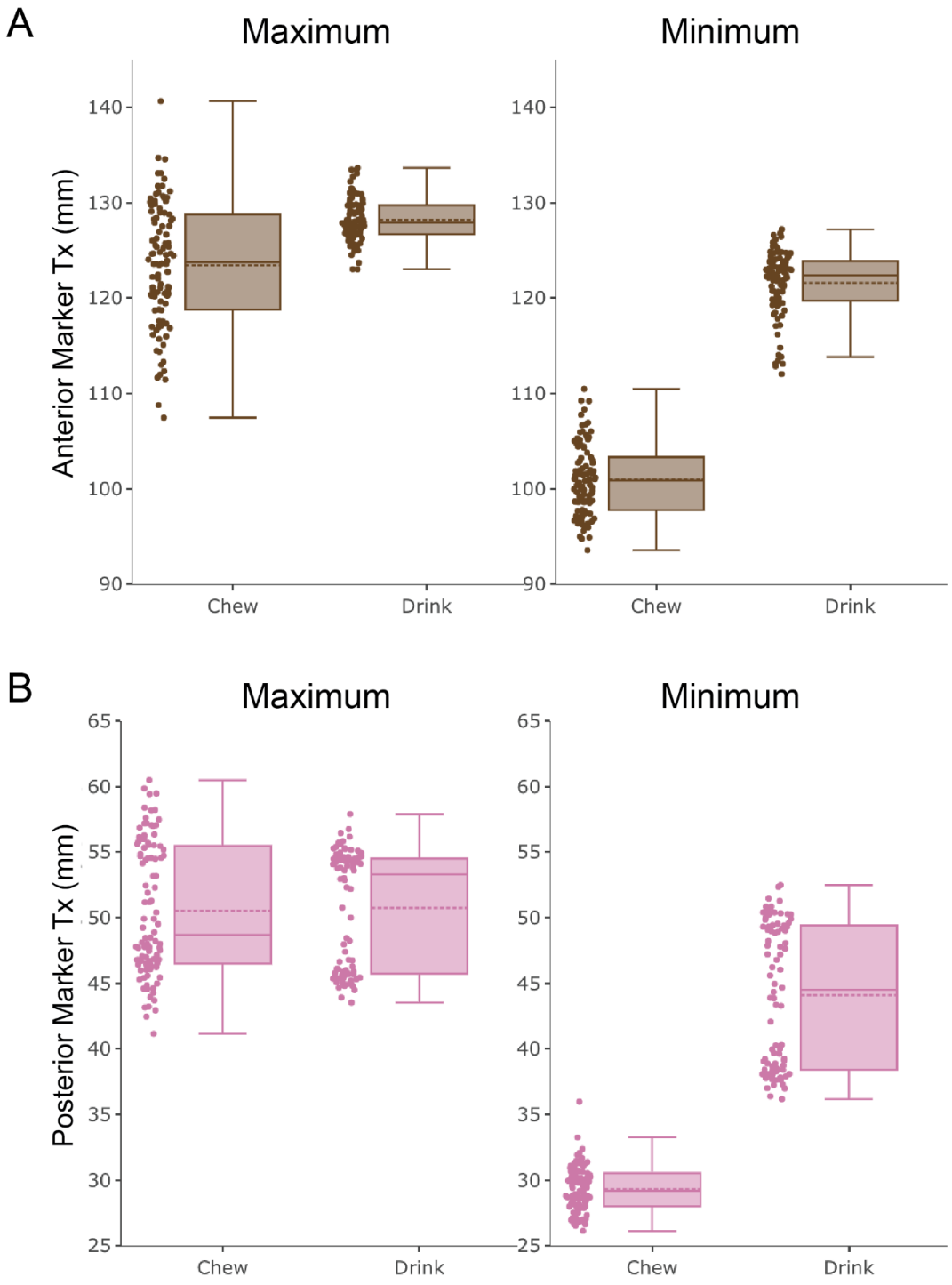

A
Maximum
Minimum
Anterior Marker Tx (mm)
140
130
120
110
100
90
Chew
Drink
B
Maximum
Minimum
Posterior Marker Tx (mm)
65
60
55
50
45
40
35
30
25
Chew
Drink

Figure 13

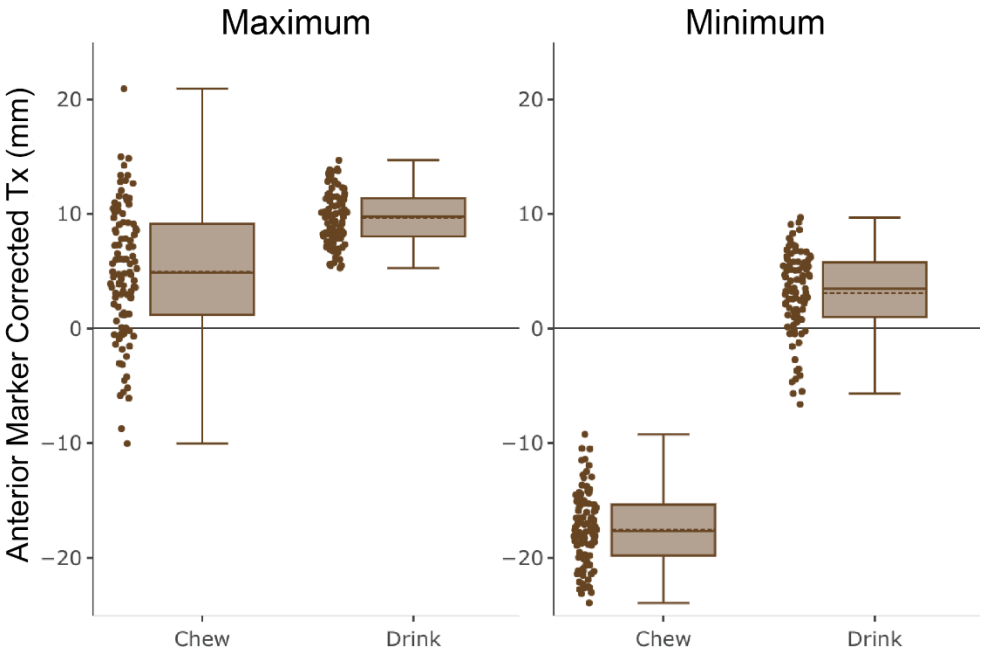

Maximum
Minimum
Anterior Marker Corrected Tx (mm)
20
10
0
−10
−20
Chew
Drink
Chew
Drink

Figure 14

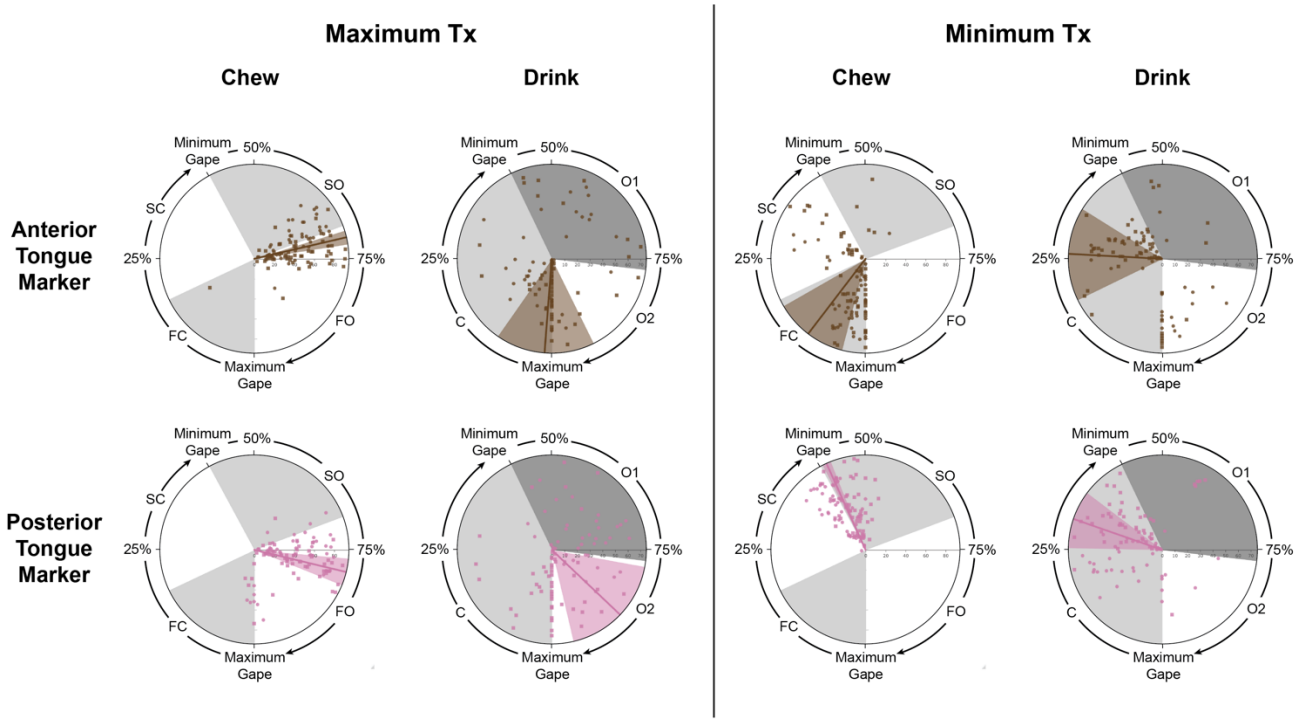

Maximum Tx
Minimum Tx
Chew
Drink
Chew
Drink
Anterior Tongue Marker
Posterior Tongue Marker
Minimum Gape
50%
SO
75%
FO
Maximum Gape
FC
25%
SC
O1
O2
C

Figure 15

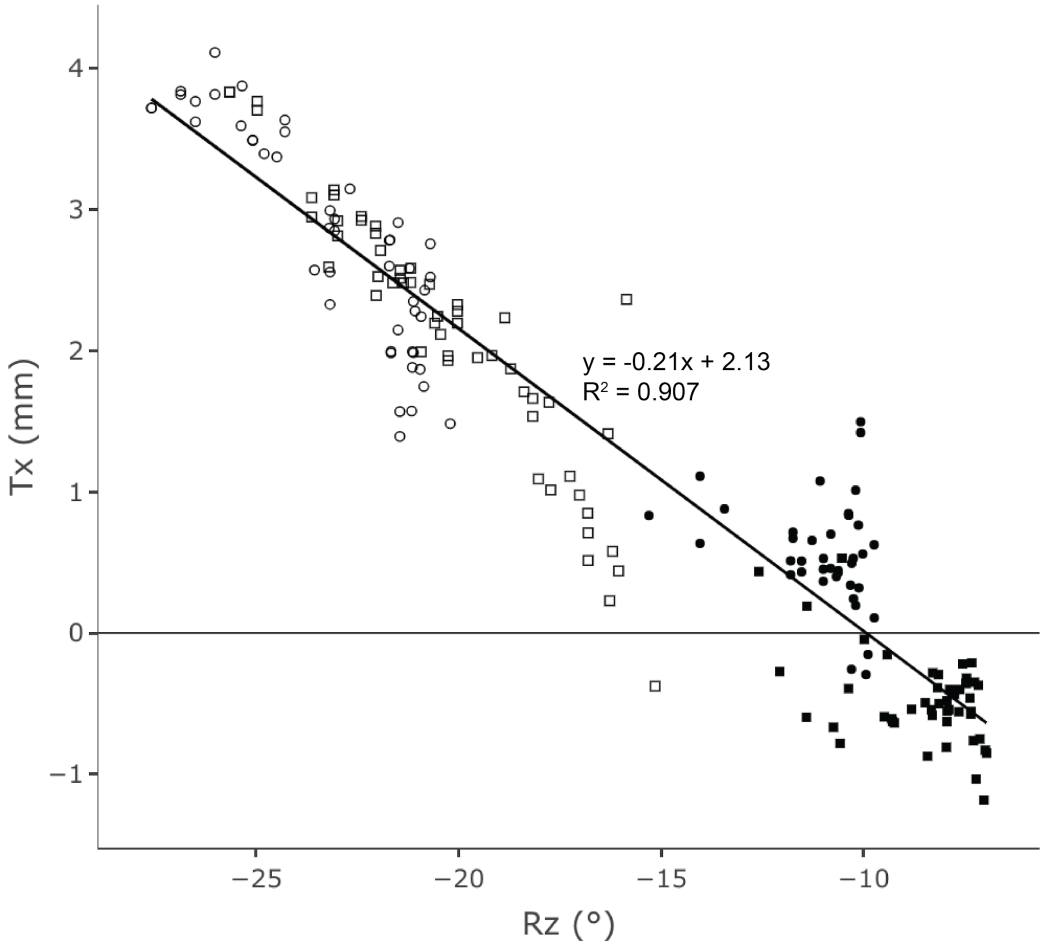
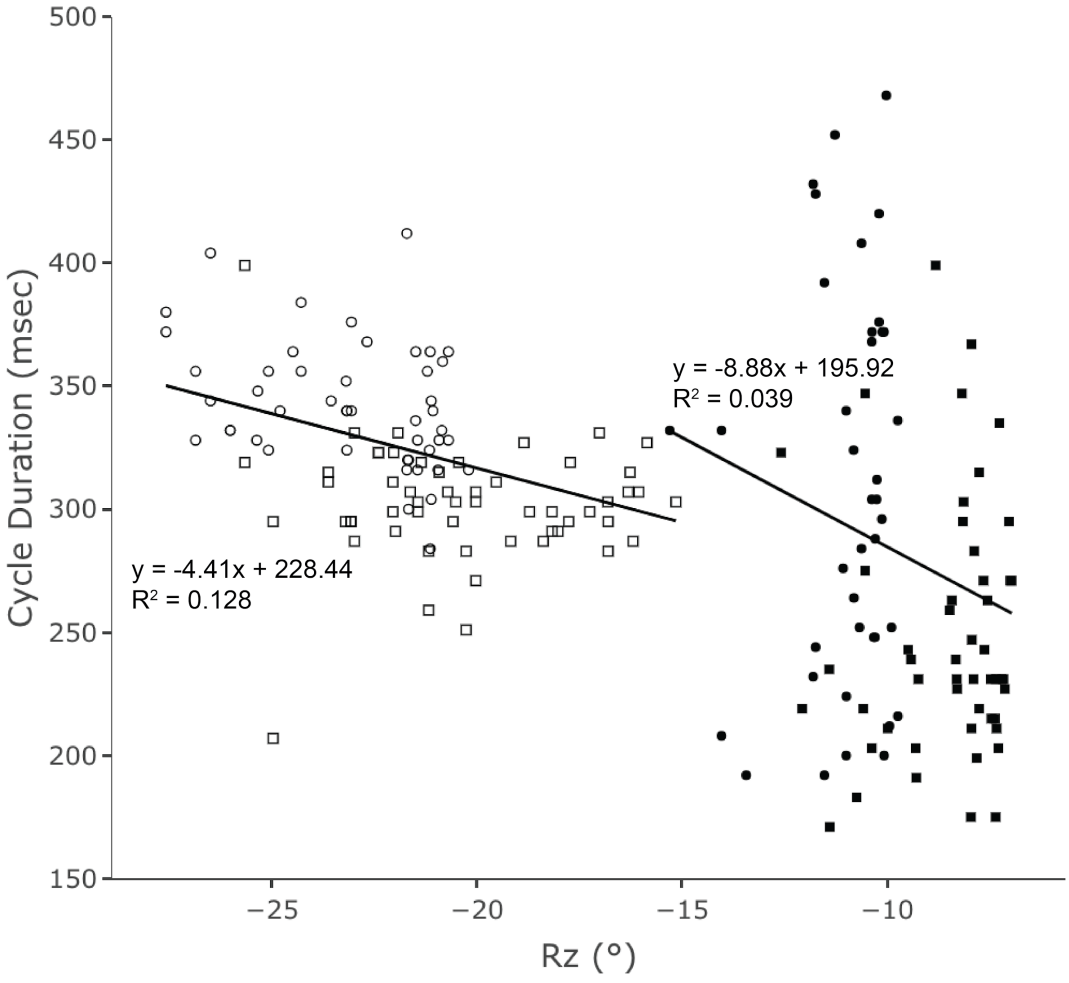


Figure 16


500
450
400
350
300
250
200
150
Cycle Duration (msec)
−25
−20
−15
−10
Rz (°)
y = -8.88x + 195.92
R² = 0.039
y = -4.41x + 228.44
R² = 0.128

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