1 **Jaw Kinematics and Tongue Protraction-Retraktion during Chewing and Drinking**
2 **in the Pig**

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

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

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24 **ABSTRACT**

25 Mastication and drinking are rhythmic and cyclic oral behaviors that require
 26 interactions between the tongue, jaw, and a food or liquid bolus, respectively. During
 27 mastication, the tongue transports and positions the bolus for breakdown between the
 28 teeth. During drinking, the tongue aids in ingestion and then transports the bolus to the
 29 oropharynx. The objective of this study is to compare jaw and tongue kinematics during
 30 chewing and drinking in pigs. We hypothesize there will be differences in jaw gape cycle
 31 dynamics and tongue protraction-retraction between behaviors. Mastication cycles had an
 32 extended slow-close phase, reflecting tooth-food-tooth contact, whereas drinking cycles
 33 had an extended slow-open phase, corresponding to tongue protrusion into the liquid.
 34 Drinking jaw movements were of lower magnitude for all degrees of freedom examined
 35 (jaw protraction, yaw, and pitch), and were bilaterally symmetrical with virtually no yaw.
 36 The magnitude of tongue protraction-retraction (Tx) was greater during mastication than
 37 drinking, but there were minimal differences in the timing of maximum and minimum
 38 tongue Tx relative to the jaw gape cycle between behaviors. However, during drinking,
 39 the tongue tip is often located outside the oral cavity for the entire cycle, leading to
 40 differences in behaviors in the timing of anterior marker maximum tongue Tx. This
 41 demonstrates that there is variation in tongue-jaw coordination between behaviors. These
 42 results show that jaw and tongue movements vary significantly between mastication and
 43 drinking, which hint at differences in the central control of these behaviors.

44 **INTRODUCTION**

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

59 Despite these fundamental differences, mastication and drinking are both
60 accomplished by coordinated and rhythmic movements of the tongue and jaw controlled
61 by the central and peripheral nervous systems. A central pattern generator (CPG) in the
62 brainstem drives masticatory rhythm (Dellow and Lund 1971; Nozaki et al., 1986). The
63 output of the masticatory CPG is modulated by feedback from the periodontal ligaments,
64 jaw and orofacial muscle spindles, and tongue mechanoreceptors in order to correctly
65 position food for processing and adjust force output (Lund and Kolta 2005; Lund and
66 Kolta 2006; Takahashi et al., 2007; Trulsson 2007; Trulsson and Johansson 2002).

67 Although extensive modulation of the CPG adjusts movements as the food is chewed
68 (e.g., Davis 2014; Dotsch and Dantuma 1989; Iriarte-Diaz et al., 2011; Thexton and
69 Crompton 1989; Weijs and De Jongh 1977), gape cycles during mastication are highly
70 rhythmic (Ross et al., 2007a,b, 2010, 2017). Similar CPGs regulating rhythmicity have
71 been observed for licking, lapping, and sucking (Barlow 2009; Boughter et al., 2012;
72 Nakamura et al., 1999; Travers et al., 1997), but with contributions from different cortical
73 areas than for mastication (Iriki et al., 1988). While less studied, there is evidence to
74 suggest that modulation of the CPG involved in drinking also occurs. For example,
75 licking frequency in rats is influenced by experimental and environmental conditions
76 (Weijnen 1998).

77 Whereas there is a general understanding of the changes in CNS connections
78 between cortical and brainstem areas underlying the maturation from drinking in infants
79 (i.e., suckling) to chewing (Iriki et al., 1988) as well as the kinematic changes across this
80 shift (German et al., 1992, 2006; German and Crompton 1996, 2000; Westneat and Hall
81 1992), comparatively less is known about the differences and similarities between
82 mastication and non-suckling drinking kinematics and motor control. Studies on the cat
83 (Hiemae et al., 1978; Thexton and McGarrick 1988, 1989) and the opossum (Crompton
84 1989) have compared jaw and tongue movements during mastication and lapping but
85 only one study, on pigs, has compared mastication and sucking in behaviorally mature
86 animals (Liu et al., 2009). This study, however, focuses specifically on tongue internal
87 deformations rather than positional changes relative to the oral cavity.

88 These previous comparisons demonstrate that during mastication, the tongue
89 positions the bolus along the toothrow for processing, usually unilaterally. When the jaw

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

105 The goal of the present study is to compare jaw and tongue kinematics during
 106 mastication and sucking in the pig (*Sus scrofa*, Linnaeus 1758) using XROMM with
 107 additional soft tissue markers in the tongue. First, we will determine whether both
 108 behaviors use the same degrees of freedom during their respective gape cycles. Previous
 109 studies have demonstrated that two rotations, jaw pitch and jaw yaw, and anteroposterior
 110 translation (i.e., jaw protraction-retraction) are used during mastication (Brainerd et al.,
 111 2010; Menegaz et al., 2015; Montuelle et al., 2020a). Whereas jaw pitch reflects jaw
 112 opening and closing, jaw yaw reflects rotation about a vertical axis contributing to the

113 characteristic “sidedness” of mastication. We hypothesize that both behaviors will utilize
114 similar magnitudes of jaw pitch and anteroposterior translation, but jaw yaw will be
115 absent during sucking because no sided interaction between the teeth and the aliquot is
116 expected.

117 Second, we compare the temporal dynamics of gape cycles during both behaviors.
118 We hypothesize that masticatory cycles will be longer and more variable than drinking
119 cycles, reflecting the changing properties of the bolus throughout a chewing sequence.
120 This variability is expected to extend to intracycle phases (e.g., fast closing, slow
121 closing). Additionally, we hypothesize that the jaw opening phases of drinking cycles
122 will be longer than those of masticatory cycles due to pronounced extraoral excursions of
123 the anterior tongue during jaw opening.

124 Finally, we compare protraction and retraction movements of the tongue during
125 chewing and drinking and relate these movements to the temporal dynamics of the gape
126 cycle. We hypothesize that drinking involves higher magnitudes of tongue protraction-
127 retraction than chewing in order to ingest and transport liquid to the oropharynx.
128 However, because injury to the tongue can occur if jaw and tongue movements are not
129 coordinated (Montuelle et al., 2019, 2020b), we hypothesize that the timing of protraction
130 and retraction relative to the gape cycle is similar between the two behaviors and has low
131 variability.

132 By comparing jaw and tongue movements during mastication and drinking, this
133 study facilitates a better understanding of the dynamic control of oral behavior variation
134 driven by interactions between central (e.g., CPGs, premotor cortex, sensorimotor cortex)
135 and peripheral (e.g., orofacial mechanoreceptors) components of the nervous system.

136 Because mammals exhibit two types of rhythmic drinking behaviors throughout their
137 lifespan (i.e., suckling and either lapping, licking, or sucking), any similarities in the
138 kinematics of mastication and drinking in weaned animals may indicate more overlap in
139 some aspects of the central control of these behaviors or similarities in their modulation,
140 despite differences in bolus properties or position.

141

142 **MATERIALS AND METHODS**

143 ***Study Design, Surgery, CT Scans, and Data Collection***

144 Jaw movements in two 3-month-old female Hampshire-cross pigs (ID #s 20 and
145 21) were quantified using marker-based X-ray Reconstruction of Moving Morphology
146 (XROMM) (Brainerd et al., 2010). In each animal, 5 to 7 radiopaque tantalum markers
147 (Bal-Tec, Los Angeles, CA, USA, 1.6 mm diameter) were surgically implanted in the
148 skull and jaw while animals were under isoflurane anesthesia (2-5%). An additional 17
149 markers were placed in the tongue, with only the anterior and posterior markers used in
150 this study (see below). After 24-hours of recovery, biplanar fluoroscopy videos were
151 recorded at 250fps using synchronized high-speed digital cameras (Oqus 310, Qualisys,
152 Göteborg, Sweden) while the animals were feeding or drinking. During recording
153 sessions, animals were offered 2cm x 2cm x 1cm cubes of apple or 475 ml of apple juice.
154 Prior to each session, perforated metal sheets (part number 9255T641, McMaster-Carr,
155 Robinson, NJ, USA) use for distortion correction and a custom Lego® calibration cube
156 were imaged in each fluoroscopy view to aid in undistorting and calibrating the videos,
157 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. 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

181 rotations and translations of the jaw relative to the skull. All axes are perpendicular to
182 each other with the x-axis running anteroposterior in the midline, the y-axis oriented
183 dorsoventrally, and the z-axis oriented along the mediolateral plane running through both
184 condyles (Figure 1A). Both a translation (T) and a rotation (R) is possible about each of
185 these axes, creating a potential for six degrees of freedom (DoF) describing rigid body
186 kinematics: Tx, Ty, Tz, Rx, Ry, Rz.

187 Displacement of the tongue markers were measured relative to a jaw anatomical
188 coordinate system (ACS) (Figure 1B). This system was a more ventrally oriented
189 coordinate system, with the xy- and yz-planes in line with the JCS used to calculate rigid
190 body translations and rotations, but with the xz-plane shifted dorsally so that it is
191 positioned along the hard palate. This allows for the calculation of movements of the
192 anterior and posterior tongue markers (Figure 1C) relative to the jaw while eliminating
193 the influence of gape on translation in the x-dimension. Unadjusted tongue marker Tx
194 values (anteroposterior translation: protraction-retraction) indicate displacement from the
195 jaw ACS. Additionally, Tx of the anterior tongue marker was also adjusted so that the tip
196 of the right central incisor defined the zero-position in the x-dimension (Figure 1C). In
197 this context, positive Tx values indicate the anterior tongue marker being located outside
198 the oral cavity, whereas negative Tx values indicate that it is located within the oral
199 cavity. Note that this is only approximate as the soft tissues surrounding the oral opening
200 (e.g., lips) are not accounted for in the rigid body motion.

201 After euthanasia, the frozen head of each animal was imaged within the calibrated
202 c-arm space. Movements of the markers were then analyzed following the same
203 XROMM workflow as above. These videos were used to calculate precision thresholds

204 for each of the 6 DoF of rigid body motion (3 translations and 3 rotations about each of
205 the 3 JCS axes). As no movement between the skull and the jaw is expected in the frozen
206 specimen, any change quantified in any DoF is interpreted as digitizing error and/or error
207 in the data collection workflow, such as suboptimal bead placement. The sequence mean
208 of each DoF $\pm$ the precision value for each individual determines the threshold for
209 determining jaw movements that exceed error and can be interpreted as real biological
210 motion. Precision thresholds for each animal are provided in Supplemental Table 1.

211 Waves representing the DoF that exceeded the precision thresholds along with the
212 waves representing tongue protraction-retraction were then analyzed in a custom
213 MATLAB script (FeedCycle: Dr. Brad Chadwell, Idaho College of Osteopathic
214 Medicine) that uses Rz (jaw pitch), the second derivative of Rz (jaw pitch acceleration),
215 and Ry (jaw yaw) to identify key parameters of the gape cycle automatically. Individual
216 cycles were defined from one instance of minimum Rz (i.e., maximum gape) to the
217 following instance of minimum Rz. Within each cycle, maximum Rz (i.e., minimum
218 gape) was used to determine the transition from jaw close to jaw open. The maximum
219 negative value (i.e., deceleration) of the second derivative of Rz was then used to divide
220 opening and closing into its constituent phases: fast close (FC), slow close (SC), slow
221 open (SO), and fast open (FO). The partitioning of gape cycles into phases based on the
222 acceleration of Rz revealed differences between mastication and drinking that impacted
223 subsequent analysis (Figure 1D). The four standard phases were observed in chewing
224 cycles (i.e., FC, SC, SO, and FO), whereas only three phases were detected in drinking
225 cycles: one closing phase (C) and 2 opening phases (hereafter called O1 and O2) (Figure
226 1D). Because of these differences, we compared the phases between behaviors

227 corresponding in the directionality (i.e., opening or closing) and acceleration of Rz. Thus,
 228 FC of mastication was compared to the single closing phase of sucking because of the
 229 comparable velocity of jaw closing. For opening, phases were compared based on their
 230 order of occurrence, i.e., SO and FO were compared to O1 and O2, respectively, given
 231 their presumed functionality in the context of the gape cycle.

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

237 In the feeding dataset used for statistical analysis, we eliminated non-chewing
 238 cycles (e.g., ingestion, stage I transport) and dropped all cycles containing a visible
 239 swallow. This resulted in 47 masticatory cycles and 40 sucking cycles for Pig 20 and 55
 240 masticatory and 50 sucking cycles for Pig 21. All statistical analyses were performed in R
 241 version 3.6.1 (R core team 2019). On magnitude variables, we used linear mixed effects
 242 models with repeated measures, with behavior as a fixed factor and individual as the
 243 random factor using the nlme (*lme: Linear and Nonlinear Mixed Effects Models*. R
 244 package version 3.1-143) and emmeans (*emmeans: Estimated Marginal Means, aka*
 245 *Least-Squares Means*) packages. Additionally, in order to compare variability in cycle
 246 durations, the coefficient of variation (CV) was calculated for each cycle and phase
 247 within each sequence of mastication or sucking. Mean and variance of timing parameters
 248 were calculated with the CircStats package (*CircStats*. R package version 0.2-6). For
 249 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
bpmme function (10,000 iterations, 2,000 burn-in, 101 seed, n.lag=3) from the package
bpmreg (*bpmreg: Bayesian 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 (Supplemental Figure 1) 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 mastication 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)
(Supplemental Figure 2). Ty and Tz occasionally exceed precision thresholds but are of
much smaller magnitude than Tx and does 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 exceed
precision thresholds for Rz and Tx (Supplemental Figure 2). This reveals that, as
hypothesized, jaw yaw (Ry) does not exceed precision values, and therefore, is not a
significant movement during drinking.

272 Compared to sucking, the magnitudes of Rz, Ry, and Tx were significantly
273 greater during mastication for whole cycles and each intra-cycle phase (Table 1). During
274 both behaviors, the jaw reaches maximum Rz (i.e., minimum gape) approximately 40%
275 into the cycle (Figure 3A). Jaw yaw (Ry) reaches a maximum just after minimum gape
276 during mastication, at which point it resets for the next cycle by switching yaw direction
277 (Figure 3B). In contrast, Ry lacked a discernible peak during sucking indicating that it is
278 a bilaterally symmetrical behavior, unlike mastication. For both behaviors, jaw retraction
279 (i.e., decreasing Tx) occurs during jaw closing whereas protraction (i.e., increasing Tx)
280 occurs during opening (Figure 3C).

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

290 The relative contribution of each phase to total gape cycle duration also differed
291 between the two behaviors (Table 1). Whereas C and O1 are proportionately longer for
292 drinking cycles than FC and SO, respectively, FO had a higher contribution to total cycle
293 duration for chewing cycles than O2 did for drinking cycles (Supplemental Figure 3).

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 is generally similar within a behavior relative to each other and relative to changes in jaw pitch but differences were observed between behaviors (Figure 4). During chewing, the anterior marker has minimal movement during jaw closing, then protracts at the start of jaw opening, followed by retraction as the jaw opens to maximum gape (Figure 4A). In contrast, the posterior marker during chewing is already in the process of retracting as the jaw begins to close from maximum gape. It then reaches minimum retraction near minimum gape, and subsequently changes direction to reach maximum protraction part of the way through opening, before it then begins to retract (Figure 4C). During drinking, the anterior tongue marker undergoes low amplitude movements, usually outside the oral cavity and may occasionally enter it before minimum gape (Figure 4B). Low amplitude movements are also observed for the posterior tongue marker (Figure 4D).

Contrary to the hypothesis, Tx displacements of the anterior tongue marker are significantly larger during chewing than during drinking (Table 2; Figure 4C,D). However, the overall Tx displacement pattern of the posterior marker is more similar between behaviors than that of the anterior marker. Although Tx displacements of the anterior tongue marker are significantly smaller during drinking, the anterior tongue marker typically has significantly higher maximum and minimum Tx values during drinking compared to chewing (Table 2; Figure 4). These results indicate that the anterior

317 part of the tongue is consistently more protracted during drinking than during chewing,
318 and that it performs greater protraction-retraction movements during chewing.
319 Nevertheless, maximum tongue protraction during chewing is quite variable and contains
320 the drinking maximum and minimum protraction-retraction values within its range. The
321 maximum protracted and retracted values of the posterior tongue marker are not
322 significantly different between behaviors, which likely reflects regional changes in
323 tongue deformation. However, during chewing the posterior marker retracts more than
324 during drinking. When Tx of the anterior marker is adjusted for displacement from the
325 lower incisor tip (Figure 5), it is clear that the anterior tongue usually protrudes outside
326 the oral cavity during chewing then retracts into the oral cavity, whereas during drinking,
327 it remains outside the oral cavity and only occasionally retracts back into the oral cavity.
328 Indeed, during chewing there is usually a single excursion outside the oral cavity during
329 jaw opening whereas during drinking, it is relatively unchanged in its position outside the
330 oral cavity through most of the cycle (Figure 2).

331 ***Timing of Tongue Protraction-Retraktion Relative to the Gape Cycle***

332 The timing of maximum and minimum Tx of both tongue markers relative to the
333 gape cycle are shown in Figure 6. During mastication, both markers reach maximum
334 protraction during FO around 75% of the way through the gape cycle, with the anterior
335 marker slightly preceding the posterior (Figure 6). During sucking, the anterior marker
336 reaches its mean maximum protraction around maximum gape (i.e., at the end of O2)
337 whereas the posterior marker reaches its mean maximum protraction earlier during O2
338 (Figure 6). However, the overall variance for the timing of maximum marker protraction
339 is high, especially compared to mastication. Only the relative timing of maximum

340 protraction of the anterior marker is statistically different between behaviors as indicated
341 by the non-overlapping HPDs (Table 3). In contrast, HPDs for the posterior tongue
342 marker overlap, indicating that the null hypotheses of no differences between behaviors
343 cannot be rejected for the posterior region of the tongue. Thus, the protraction of the
344 anterior tongue is delayed, yet more variable, during sucking compared to mastication,
345 whereas the timing of the protraction of the posterior region of the tongue is similar
346 during both behaviors.

347 During mastication, the anterior tongue marker usually reaches its maximum
348 retracted position (i.e., minimum Tx) during FC, whereas the posterior marker reaches its
349 maximum retracted position later, usually near minimum gape (Figure 6). During
350 drinking, both markers are usually fully retracted during closing, with relatively high
351 levels of variance compared to chewing. This higher variance may originate from the
352 relatively flat traces (as illustrated in Figure 4) because both locators spend a large
353 portion of the cycle at or near their respective maximum retracted position. In spite of this
354 variability, the anterior marker seems to be maximally retracted earlier during chewing
355 than during drinking, whereas the reverse is true for the posterior marker (Figure 6).
356 However, the HPD intervals for the timing of minimum Tx for both markers overlap
357 between behaviors, indicating no statistical difference (Table 3).

358

359 **DISCUSSION**

360 ***Jaw Movements during Chewing and Drinking***

361 As in chewing, the primary degree of freedom of jaw movements during drinking
362 is Rz (i.e., jaw opening-closing), but the magnitude of pitch change between the two

types of cycles is 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. 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 cycles, whereas during sucking cycles, the lower jaw never elevates beyond -5° (see Figure 4A) resulting in a relatively small change in jaw pitch during each cycle ($3.17^\circ \pm 1.2$; Table 1). Lapping in species with incomplete cheeks, such as the cat, demonstrate much larger pitch magnitudes (i.e., over 15° in the cat; Hiimeae 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 (Crompton and Musinsky 2011; Reis et al., 2010). 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 5) 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 (R_y) to facilitate unilateral chewing. Although isognathia in pigs means that both sides occlude during a single cycle (see Herring et al., 2001), there is a clear “sidedness”

386 to the behavior demonstrated by directionality in Ry during SC. This is supported by
387 asymmetrical jaw muscle motor patterns in pigs despite similarities in bone strain
388 patterns on the working- (i.e., chewing) and balancing- (i.e., non-chewing) sides (Herring
389 1976; Herring and Wineski 1986; Herring et al., 2001). In contrast, during drinking,
390 changes in jaw yaw are virtually absent throughout the entire gape cycle. This confirms
391 that drinking in pigs involves bilaterally symmetrical jaw movements, consistent with our
392 hypothesis. Bilaterally symmetrical jaw movements also occur during infant suckling in
393 the hamster (Lakars and Herring 1980), during food gathering and the initial cycles of nut
394 crushing in pigs (Menegaz et al., 2015), and they can be inferred for suckling in the pig
395 from their bilaterally symmetrical jaw muscle motor patterns (Herring 1985b).

396 Finally, previous work on pigs also shows that of the three available translational
397 DoF, jaw movements during chewing cycles only use anteroposterior (Tx) translations
398 (Brainerd et al., 2010; Menegaz et al., 2015; Montuelle et al., 2018, 2019, 2020a). We
399 show here that this is also the case for drinking cycles. Moreover, the timing of jaw
400 protraction and retraction is similar between the behaviors as hypothesized: jaw retraction
401 occurs primarily during closing and protraction occurs primarily during opening as was
402 expected. However, the magnitude of Tx is much lower during drinking because the jaw
403 is operating over a much narrower range of pitch change. This decreases the translation
404 necessary at the temporomandibular joint (TMJ). As Tx still exceeds the precision
405 threshold during drinking, and there is also linear correlation between jaw pitch and
406 protraction-retraction during both behaviors (Figure 7), this demonstrates the basic
407 translational-rotational anatomical coupling mechanism within the TMJ that is typical of
408 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 (Chen 1998; Hylander 1992; 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 due to 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 is 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, absent changes in jaw velocity through the cycle, this would extend cycle duration. However, only a weak correlation is observed in the relationship between cycle pitch magnitude and cycle duration for both behaviors (Supplemental Figure 4). 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 1; Supplemental Figure 3).

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

442 We hypothesized that opening phases would be longer during drinking than
443 chewing due to extraoral excursions of the anterior tongue during these phases. Instead,
444 total close and total open durations were similar between behaviors. There were,
445 however, differences in the absolute and relative durations of the opening phases. The
446 first opening phase was longer during drinking than chewing, and the second opening
447 phase was longer for chewing (both absolute and relative). The relative duration of
448 chewing SO decreases in pigs as food stiffness and toughness increase (Montuelle et al.,
449 2018), such that the relationship observed in this study between chewing and drinking is
450 likely to hold across other foods. Therefore, this long initial opening phase, in which the
451 oral cavity increases in volume, may be functionally relevant to the creation of the
452 pressure gradient necessary for sucking.

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

460 *Tongue Protraction-Retraction*

461 Contrary to our hypothesis, the magnitude of anterior tongue protraction and
462 retraction is higher during chewing compared to drinking. During most chewing cycles,
463 the anterior tongue marker exited the oral cavity and always retracted more into the oral
464 cavity. During drinking, however, the anterior tongue marker always leaves the oral
465 cavity but only occasionally retracts fully into it (Figure 2). This is contrary to lapping in
466 mammals with incomplete cheeks, in which the tongue always retracts into the oral cavity
467 in successive cycles (Thexton et al., 1998). Whether protraction-retraction movements of
468 the tongue are produced by movements of the tongue base or intrinsic regional
469 deformations, or both, requires further investigation.

470 When observed without fluoroscopy, pigs appear to use suction to consume
471 liquids, utilizing low amplitude, rhythmic jaw movements (Herring and Scapino 1973;
472 Thexton et al., 1998; pers. obs.). However, according to Thexton et al., (1998), pigs
473 utilize a combination of suction and lapping to transport the liquid bolus. The suction
474 component of drinking may be created by the small amounts of jaw opening (i.e.,
475 decreasing Rz) that increase the volume of the oral cavity and creating a negative

pressure within the oral cavity that draws water in. During drinking, we found that 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 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., 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 is observed for the timing of maximum and minimum Tx 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 value) during jaw closing. However, the timing of maximum Tx of the anterior tongue marker is significantly different between chewing and drinking (i.e., non-overlapping HPDs; Table 3). 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

499 anterior tongue occurs at maximum gape (100% of total cycle duration, at the O2-closing
500 transition), albeit with higher variance. This corresponds to the timing of tongue
501 protraction observed during lapping in the cat (Thexton and McGarrick 1988). Thus,
502 while there is some variability in protraction timing, the overall pattern is one that is
503 consistent with retracting the tongue as the jaw closes, when there are both functional
504 requirements associated with food or liquid transport as well as protection of the tongue
505 as the teeth approximate. This also likely reflects fundamental properties of the motor
506 control or orofacial movements: coactivation of jaw-opening with tongue-protruding
507 muscles and jaw-closing with tongue-retraction muscles, which is known to occur across
508 a variety of oral behaviors including mastication (e.g., Liu et al., 1993; Naganuma et al.,
509 2001), licking (Travers et al., 1997), and infant suckling (Thexton et al., 1998). The fact
510 that the motoneurons serving the groups of muscles coordinating tongue protrusion with
511 jaw opening as well as tongue retraction with jaw closing share premotor neurons further
512 supports our expectation (Stanek et al., 2014). Nevertheless, the more detailed analysis of
513 these movements here demonstrates anteroposterior variation in tongue protrusion
514 relative to jaw opening, a time when damage is unlikely to occur.

515 ***Central Control of Chewing and Drinking Behaviors***

516 These differences between drinking and chewing may provide insight into the
517 changes that occur as infants shift from suckling to chewing solid foods and sucking for
518 liquid ingestion. Mammalian infant suckling consists of negative pressure created by
519 suction and/or physical expression of the teat (e.g., Herring 1985a; Thexton et. al., 2004).
520 During both suckling and sucking in pigs, jaw opening appears to be the primary manner
521 in which suction is created. During both behaviors, the tongue is outside the oral cavity

522 for most of the cycle and anteroposterior tongue movements are small suggesting they
523 contribute little to the creation of suction. As the tongue does not always return to the oral
524 cavity and as the oral opening is continually submerged into the liquid, the small amount
525 of tongue retraction is unlikely to form a liquid column as in lapping. Furthermore, both
526 suckling and drinking appear to be bilaterally symmetrical (Lakars and Herring 1980), as
527 compared to chewing which is unilateral, and has clear differentiation of sidedness, both
528 in the jaw and the tongue movements (e.g., Abd-El-Malek 1955; Hiimeae and Palmer
529 2003). Chewing cycles occur at a lower frequency (3.1 vs 3.6 Hz) than drinking, and the
530 frequency of drinking falls within the range of what is observed in infant pig suckling
531 (3.5-4.4 Hz) (German et al., 1997). Therefore, drinking in adult pigs shares some
532 common attributes with infant suckling.

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

545 results suggest that there are connections but also fundamental differences in the central
546 control of sucking and chewing behaviors in pigs.

547 **CONCLUSIONS**

548 The 3D kinematics of the jaw and tongue for chewing and drinking in pigs further
549 our understanding of how these movements facilitate different oral behaviors. Drinking
550 cycles were confirmed to be non-sided and instead only utilize two DoF: jaw pitch and
551 anteroposterior translation. Chewing and drinking cycles were observed to have similar
552 relative contributions of opening and closing to a standardized gape cycle, although with
553 differing variability for each phase. Differences in tongue protraction-retraction
554 magnitudes were observed, with larger magnitudes of movements observed during
555 chewing. The timing of these movements indicates that some aspects of the tongue-jaw
556 coordination pattern are different between these behaviors. Further, sucking in adults
557 resembles infant suckling, including jaw opening to create suction and the anterior tongue
558 positioned outside the oral cavity. Therefore, drinking cycles show characteristics of both
559 chewing and infant suckling cycles, suggesting further research into the central control of
560 different oral behaviors would provide valuable insight into the development of CPGs
561 across different oral behaviors through ontogeny.

562

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570

571 **COMPETING INTERESTS**

572 No competing interests declared.

573

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581

582 **DATA AVAILABILITY**

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

TABLES

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
Magnitudes (Mean ± SD)			
Total Cycle			
Rz (deg)	20.8 ± 2.4	3.17 ± 1.2	SE = 0.276, T _{2,192} = 64.2, p < 0.0001
Ry (deg)	3.66 ± 0.79	0.708 ± 0.26	SE = 0.0859, T _{2,192} = 34.3, p < 0.0001
Tx (mm)	6.98 ± 1.3	2.08 ± 0.41	SE = 0.117, T _{2,192} = 42.0, p < 0.0001
FC/CI			
Rz (deg)	13.7 ± 3.3	2.90 ± 1.2	SE = 0.365, T _{2,192} = 29.6, p < 0.0001
Ry (deg)	1.32 ± 0.52	0.625 ± 0.28	SE = 0.0609, T _{2,192} = 11.4, p < 0.0001
Tx (mm)	4.29 ± 1.6	1.87 ± 0.59	SE = 0.159, T _{2,192} = 15.3, p < 0.0001
SC			
Rz (deg)	6.32 ± 2.7	—	—
Ry (deg)	1.15 ± 0.79	—	—
Tx (mm)	2.25 ± 0.97	—	—
SO / O1			
Rz (deg)	6.12 ± 5.1	1.43 ± 0.67	SE = 0.540, T _{2,192} = 8.68, p < 0.0001
Ry (deg)	2.20 ± 0.97	0.431 ± 0.24	SE = 0.105, T _{2,192} = 16.9, p < 0.0001
Tx (mm)	2.68 ± 2.0	0.976 ± 0.61	SE = 0.223, T _{2,192} = 7.65, p < 0.0001
FO / O2			
Rz (deg)	13.7 ± 5.3	1.29 ± 0.89	SE = 0.8564, T _{2,192} = 22.1, p < 0.0001
Ry (deg)	1.89 ± 1.2	0.345 ± 0.21	SE = 0.126, T _{2,192} = 12.2, p < 0.0001
Tx (mm)	3.95 ± 2.3	0.963 ± 0.54	SE = 0.235, T _{2,192} = 12.8, p < 0.0001
Absolute Durations (msecs, Mean ± SD (CV))			
Total Cycle	323 ± 31 (9.50)	281 ± 82 (29.1)	SE = 8.04, T _{2,192} = 5.17, p < 0.0001
FC / C	57.7 ± 18 (30.9)	120 ± 51 (42.3)	SE = 5.25, T _{2,192} = -12.0, p < 0.0001
SC	78.3 ± 25 (31.8)	—	—
SO / O1	90.6 ± 57 (63.0)	97.5 ± 52 (53.1)	SE = 7.73, T _{2,192} = -0.930, p = 0.354
FO / O2	97.1 ± 53 (54.2)	65.0 ± 54 (83.4)	SE = 7.74, T _{2,192} = 4.15, p < 0.0001
Relative Durations (% Mean ± SD (CV))			
FC / C	18.0 ± 5.8 (32.5)	42.9 ± 13 (29.3)	SE = 1.39, T _{2,192} = -17.9, p < 0.0001
SC	24.1 ± 7.4 (30.9)	—	—
SO / O1	27.7 ± 17 (59.5)	34.5 ± 14 (41.2)	SE = 2.24, T _{2,192} = -3.02, p = 0.0028
FO / O2	30.1 ± 16 (53.2)	23.1 ± 14 (62.1)	SE = 2.20, T _{2,192} = 3.205, p = 0.0016

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

	Chew	Drink	Model by Behavior
Magnitude (mm) ± SD			
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 Marker	SE = 0.726, $T_{2,192} = 1.73$, $p = 0.0847$	SE = 0.425, $T_{2,192} = -0.137$, $p = 0.892$	
Maximum (mm) ± SD			
Anterior	123 ± 6.4	128 ± 2.3	SE = 0.554, $T_{2,192} = -4.64$, $p < 0.0001$
Posterior	50.5 ± 5.0	50.7 ± 4.5	SE = 0.288, $T_{2,192} = -1.69$, $p = 0.0927$
Model by Marker	SE = 0.806, $T_{2,192} = 90.5$, $p < 0.0001$	SE = 0.450, $T_{2,192} = 172$, $p < 0.0001$	
Minimum (mm) ± SD			
Anterior	101 ± 3.7	122 ± 3.5	SE = 0.492, $T_{2,192} = -42.0$, $p < 0.0001$
Posterior	29.3 ± 1.7	44.1 ± 5.4	SE = 0.372, $T_{2,192} = -39.5$, $p < 0.0001$
Model by Marker	SE = 0.398, $T_{2,192} = 180$, $p < 0.0001$	SE = 0.572, $T_{2,192} = 136$, $p < 0.0001$	

Table 3. Results of the circular mixed effects model for the timing of maximum tongue Tx

	Posterior Mean $\pm$ sd (start, end)		Posterior Mean $\pm$ sd (start, end)	
	Chew Cycles	Drink Cycles	Chew Cycles	Drink Cycles
Anterior	71.1 $\pm$ 2.7 (65.9, 76.4)	1.7 $\pm$ 6.7 (93.9, 14.2)	8.6 $\pm$ 4.5 (2.5, 16.1)	26.4 $\pm$ 6.2 (12.9, 40.0)
Posterior	77.5 $\pm$ 4.5 (67.5, 86.8)	86.7 $\pm$ 10.4 (55.1, 0.6)	43.1 $\pm$ 3.4 (38.7, 46.9)	29.2 $\pm$ 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). (D) 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 2. 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 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 minimum Rz values, or the transition between cycles.

Figure 3. 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 4. 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 5. 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 positive Tx indicates the marker is outside the oral cavity whereas negative Tx indicates it is within the oral cavity.

Figure 6. 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 7. 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 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

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