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Internal kinematics of the tongue in relation to muscle activity and jaw movement in the pig

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SUMMARY

To explore the coordinative characteristics of tongue deformation, muscle activity and jaw movement during feeding, six ultrasonic crystals were implanted into the tongue body of ten 12-week-old Yucatan minipigs 1 week before the recording. These crystals formed a wedge-shaped configuration to allow recording dimensional changes in lengths, anterior and posterior widths and posterior thicknesses of the tongue body during feeding. Wire electromyographic activities (EMG) of superior and inferior longitudinalis, verticalis/transversus, genioglossus, styloglossus, masseter and digastricus and jaw movements were recorded simultaneously. Signals from these three sources were synchronized for real-time analyses. The results indicate: (i) dimensional changes were stereotypical in relation to each cycle of all three feeding behaviours; (ii) during chewing, expansion of tongue widths mainly occurred in the occlusal phase of jaw movement and was less coupled with the activity of tongue muscles, but the expansions of length and thickness were seen in the opening and closing phases and were better coupled with the activity of tongue muscles ($P < 0.05$); (iii) ingestion was characterized by the two-phased jaw opening, early expansion of anterior width prior to the occlusal phase and strong associations between tongue deformation and muscle activity; (iv) during drinking, the duration of the opening and closing phases was significantly prolonged ($P < 0.01$), the durations of tongue widening and lengthening were significantly shortened ($P < 0.05$) and anterior widening was predominant in the opening rather than in the closing or occlusal phases as compared with chewing and ingestion; and (v) the intrinsic tongue muscles did not show more or stronger correlations with the tongue deformation than did the extrinsic tongue muscles. These results suggest that (i) regional widening, lengthening and thickening of the tongue body occurs sequentially in relation to jaw movement phases, but the initiation of tongue dimensional expansions does not correspond with the activation of tongue muscles simultaneously; (ii) there is a better coupling between tongue deformations and tongue muscle activations in the sagittal (lengthening and thickening) than the transverse (widening) planes; and (iii) the patterns and ranges of tongue deformation and their relations to muscle activity and jaw movement are task-specific and the expansion magnitudes of tongue deformation does not have closer correlations with the amount of EMG activity in the intrinsic than the extrinsic tongue or jaw muscles.

Keywords

tongue deformation; electromyography; jaw movement; ultrasound; feeding; pig

Introduction

The tongue performs function by displacing its position multidirectionally and altering its shape multidimensionally through the sequential contraction of its musculature. As a hydrostat muscular organ with incompressible properties (1), the tongue kinematics is restricted neither to the simple protrusion-retrusion and/or descending-ascending axes nor vertical rotation like that seen for the jaw, but involves complex shape and regional volumetric changes during function. These changes are produced by sequential muscular activity and accompanied by jaw movement (2–6).

Studying tongue kinematics and biomechanics by observations of its shape (deformation) or position (movement) changes during function has been challenged by its difficult accessibility and architectural complexity. Methods have included photography (7), video fluoroscopy (8) or cineradiography (9), ultra-sound (10, 11), magnetic resonance imaging (MRI) (12, 13) and mathematical modelling (3). However, few studies have addressed tongue internal kinematics in relation to the concomitance of jaw movement and the contributing activity of tongue and jaw muscles. The possible reason for this absence is mainly due to the lack of an appropriate approach to measure internal deformation of the tongue, muscular activity and jaw movement during function in a real-time manner. Understanding these characteristics and relationships would greatly improve our knowledge of motor control, kinematics, biomechanics and functional capacity of the tongue.

We previously reported the relationships of tongue deformation, muscle activity and jaw movement (14). However, that brief report has several critical shortcomings: (i) data were collected immediately after the implantation of ultrasonic crystals in the tongue (acute experiment), thus the surgical injury and pain could have affected the normal kinematics of the tongue; (ii) only chewing sequences were examined; and (iii) the sample sizes were very limited. To better understand tongue internal kinematics and to obtain high quality of functional data in a 'normal' setting, we took a further step to carry out this chronic study to overcome the above-mentioned pitfalls and to address the following new questions: (i) how do contractions of the tongue and jaw muscles lead to specific tongue deformations in various dimensions (lengths, widths and thicknesses) and regions (anterior vs. posterior, dorsal vs. ventral) during various feeding behaviours and (ii) how do these tongue deformational changes coordinate with different phases of jaw movement?

Based on studies on tongue deformation and electromyography (EMG) of the tongue and jaw muscles (15, 16), we found that (i) the EMG patterns of tongue muscles are chewing-side related; (ii) integrated EMG (IEMG) of the intrinsic tongue muscles are greater than those of the extrinsic tongue and jaw muscles and (iii) dimensional expansions of the tongue are larger in the anterior width (AW) and posterior thickness than in the length and posterior ventral and dorsal widths. Inspired by these results, we further hypothesized that (i) during chewing, tongue dimensional expansions in the sagittal plane (lengthening and thickening) are predominant during jaw opening and closing, whereas those in the transverse planes (widening) are predominant during occlusal phase; (ii) tongue dimensional expansions are symmetric during ingestion, drinking and swallowing but side-dependent during chewing; (iii) the reversal of expansion-compression of tongue dimensional changes is not directly driven by the activation of the tongue muscles; and (iv) the ranges of dimensional changes

of the tongue are function-dependent, rather than proportional to the EMG amplitudes in the tongue muscles.

Materials and methods

Animal care and implantation surgery

Ten 12-week-old Yucatan miniature pigs (five of each gender, the range of body weight: 9–12 kg) were used. The experimental protocol was approved by Institutional Animal Care and Use Committee of the University of Washington. For acclimation of pigs to laboratory, daily training was performed throughout the experimental period.

One week before the recording, pigs received an aseptic surgery to implant a sonomicrometric skin button set.* Under isoflurane anaesthesia through intubation, a submandibular incision along the midline was first made. A long-beak haemostat was used to create a tunnel to reach the designed crystal location (Fig. 1), which was confirmed by manual palpation intraorally. The b-barb crystal (2 mm in diameter, Fig. 1, insert) was delivered to the target location through the tunnel using another long-beak straight haemostat. The crystal was stabilized in the place through its barbs and by suturing the proximal end of its leading wire onto the adjacent tongue tissue using an absorbable suture (Gut 4-0). No intra-oral incision or exposure was made for the crystal implantation. Then, a subcutaneous tunnel was created from the submandibular to the right back, and the leading wires of implanted crystals were led to the back through this tunnel and were exited from the back 10 cm posterior to the occipital protuberance where a female interface (skin button, Fig. 1, insert) was secured to skin by 2-0 silk sutures. The locations of 6 implanted crystals and the composed wedge-shaped configuration in the tongue body are illustrated in Fig. 1. Similar to the acute studies published previously (6, 16, 17), the following seven crystal pairs were selected from this configuration to represent seven dimensions of the tongue body: AW (#1–2), posterior dorsal and ventral widths (PDW and PVW, #3–4 and #5–6), right and left length (RL and LL, #1–3 and #2–4) and right and left posterior thickness (RT and LT, #3–5 and #4–6). The initial distances of these seven crystal pairs were measured using a digital calliper at the completion of the implantation. Antibiotic (Clavamox) was administered 1 day before and for 5 days post-surgery.

Placement of EMG electrodes and jaw markers

The recording was performed 7 days after the surgery and the pig was deprived of food for 24 h before recording. On the recording day, the pig was first anaesthetized by isoflurane through a nostril mask. Eight pairs of nickel–chromium wire electrodes (0.05 mm, 1 mm bared tip and 3 mm interpolar distance) were inserted into the seven tongue and jaw muscles along their fibre directions by 25G needles, i.e. right genioglossus (GG), styloglossus (SG), superior and inferior longitudinalis (SL and IL), verticalis/transversus (V/T), digastricus (DI) and right and left masseters (RMA and LMA). Fibres of the verticalis and transversus are extensively interwoven, thus these two intrinsic tongue muscles were not discriminated. The accuracy of targeting electrodes was verified through the back stimulation and cadaver testing which were detailed elsewhere (15).

Four fluorescent markers were glued on the skin of upper and lower lips, two of each, for digital videotaping of jaw movement. These markers formed the upper and lower segments parallel to the occlusal plane (Fig. 1). Finally, the skin button (female interface with the leading wires of implanted crystals) was connected to the sonomicrometric system through a male interface cable.

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Data recording and signal synchronization

After these placements, the distances of implanted crystal pairs were measured when the tongue was manipulated at rest to validate their stability over time by comparing with the initial calliper registers obtained at the end of the implantation surgery. Then, anaesthesia was ceased and the pig was allowed to regain consciousness and fed regular pig chow and water. Electromyography and crystal signals were sampled at the rate of 500 Hz by a computer running Acqknowledge III (MP100; Biopac System Inc, Goleta, CA, USA) for 15–20 min. Of the seven crystal pairs, only four were selected to be synchronized with EMG and jaw movement due to the limitation of the maximal output analogue channels provided by the sonomicrometric system.

In addition to the above sampling by Acqknowledge III, EMG signals from bilateral masseters (LMA and RMA) were also recorded simultaneously by another computer running Motus system (Peak Performance Technologies Inc., Centennial, CO, USA). To synchronize EMG signals with jaw movements captured using a digital video camera,[†] an Event & Video Control and Analog to Digital Interface was applied to trigger the starting point of both EMG and jaw movement. Ingestion episodes were distinguished from chewing sequences under visual inspection through on-line marking during mastication session and drinking session was viewed when water was offered in a transparent glass container. After recording, the skin button was separated from the male connector of the system, but the implanted crystals still stayed in place. The pig was sent back to the pen after EMG electrodes and fluorescent makers were removed.

Off-line data processing and statistical analyses

Based on the consistent rate and stereotypical presentation, consecutive 15–20 chewing, ingestion or drinking cycles of a stable sequence from each animal were selected for off-line data processing. Solid food swallowing could not be identified during mastication, but liquid swallowing was defined every 3–4 cycles during drinking as described previously (16). Captured jaw movement images were first digitized using Peak Motus program. The angulations of the separation between the two segments composed of four fluorescent markers were used to calculate the degrees of jaw opening (gape, Fig. 1). Jaw opening, closing and occlusal phases (power stroke) were defined and marked by looking at the motions of the lower markers in relation to the upper markers from successive frame replaying as detailed previously (15) and these phases were superimposed on each channel of the synchronized EMG signals. The total cycle length was calculated from the time point of the maximal opening (MOP, i.e. beginning of jaw closing) to the time point of the next MOP, which was defined as the rate of a given feeding sequence and was taken as 100% for all other timing calculations. Thus, timing measurements from all sources were standardized to the proportion (%) of the corresponding total cycle length. Because EMGs of LMA and RMA were simultaneously sampled by both Acqknowledge III and Motus systems and also synchronized with jaw movements, the EMG timings of other muscles and the timings of the tongue deformation (crystal signals) in relation to jaw movement phases were calculated on the basis of taking the timings of LMA and RMA as the common references.

Band-pass (60–250 Hz) and low-pass filtering (30 Hz) were applied for EMG and crystal signals respectively. For chewing cycles, the working and balancing sides were identified by looking at the differences of timing and amplitude between bilateral MAs, i.e. the side showing higher amplitude and delayed onset was considered as a working side (18, 19). However, no side discrimination was made for both ingestion and drinking due to their symmetric nature in jaw movement. Some irregular transitional cycles were often seen

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between chewing and ingestion episodes during a masticatory sequence (16), which were excluded. Because the baseline of crystal signals was not stable, their time points and magnitudes were calculated by measuring the difference between the peak (maximum) and valley (minimum) from each selected crystal pairs. The polarity of dimensional change (increase or decrease) was determined by identifying the first peak/valley point to the second peak/valley point within one cycle as described previously (16). Therefore, the following variables were used to analyse each cycles of chewing, ingestion or drinking: (i) onset and offset (ms): starting and ending time points of the EMG burst or the increase (expansion) of tongue dimension; (ii) duration (ms): time length of the EMG burst or the increase of tongue dimension; (iii) IEMG ($\mu\text{V s}^{-1}$): calculated by integrating the signal over a specified interval of time and subsequently forming a time series of the integrated values, reflecting the amount of EMG activity per time unit, (iv) magnitudes (mm): the distance between each valley and peak of a paired crystal signal, reflecting the range of tongue dimensional change. The timing (onset and duration) and magnitude variables were further converted to the ratios proportional to the corresponding total cycle length and the initial distance of each crystal pair measured at the implantation (both as 100%) respectively.

Because data were asymmetrically distributed, Kruskal–Wallis H test was used to examine the differences across multiple variables, followed by Mann–Whitney *U*-test for pair-wise comparisons. The differences of the same crystal EMG signals between the working and balancing sides during chewing were examined using Mann–Whitney *U*-test. The associations between the range of tongue dimensional changes (magnitudes of crystal signals) and amount of muscular activities per unit time (IEMG) were assessed by Spearman's correlation. The significant level was set as $P < 0.05$.

Results

Patterns of jaw movement and tongue dimensional changes

Masticatory sequences were composed of multiple chewing and ingestion episodes interposed by a few of short transitional periods characterized by 1–4 less rhythmic, irregular and extended cycles (16). Each chewing and ingestion episode contained a number of consecutive and stereotypical cycles, 10–50 for chewing and 5–20 for ingestion. Ingestion episodes were easily distinguished from chewing episodes by the observation. However, puncture-crushing cycles could not be distinguished from chewing sequences as previously noted (20). During drinking, the tip of snout was submerged in the water and jaw movement was almost invisible. Jaw movement rate was significantly faster and jaw opening gape was significantly smaller during ingestion than chewing. However, the rate was only slightly faster during drinking than chewing, along with a significantly reduced opening gape of jaw movement for drinking (Table 1, upper panel).

A chewing cycle was composed of jaw opening, closing and occlusal phases and occlusal phase took up almost the half of the total cycle length (45.1%, Table 1). The beginnings of occlusal and opening phases were close to the onset and offset of MA activity, respectively, and the transition from jaw opening to closing was in the late half of the cessation period of MA activity (Fig. 2a). The two-phased jaw opening was seen during ingestion with a significantly shortened occlusal phase and the first opening phase was significantly longer than the second one (Table 1). Masseter activity started prior to or in the occlusal phase and extended to the first opening phase (Fig. 2b). The drinking cycles mainly consisted of opening and closing phases (48.0% and 37.0% respectively), but a short occlusal phase (15.0%) was still recognizable (Table 1). Unlike chewing and ingestion, MA activity started at the late jaw closing phase (Fig. 2c).

Stereotypical sequences of tongue dimensional changes were seen in accordance with cyclic EMG bursts of the tongue and jaw muscles and rhythmic jaw movement during feeding. However, these dimensional changes were less smooth with two or more fluctuations as compared with jaw movement (Figs 3–5). The difference of tongue dimensional changes between working and balancing sides of chewing was unidentifiable (Figs 3 and 6). During ingestion, the magnitude of tongue length change (RL) was greatly enhanced as compared with that during chewing (Fig. 4). During drinking, activity bursts in all tongue muscles were extended along with enhanced dimensional changes in the posterior width of the tongue (PDW and PVW). In particular, strong EMG activity bursts of SG appeared periodically every 3–4 drinking cycles, indicating swallowing episodes. The time length of these swallowing episodes (~427 ms) was close to the rate of drinking (~445 ms, Table 1), along with sustained compression in the posterior widths (PVW and PDW, Fig. 5).

Tongue dimensional changes relative to jaw movement

The timing relationships between tongue dimensional changes and EMG activities in relation to jaw movement phases during chewing, ingestion and drinking were shown in Figs 6, 8 and 9 respectively. It is clearly shown that during chewing, the majority of width expansion (AW, PVW and PDW) occurred in the occlusal through early jaw opening phases, whereas expansions in the length and thickness (LENG and THICK) were in the opening through late jaw closing phases. Posterior ventral width started to expand at the late closing and peaked at the late occlusal phases and the duration of its expansion was significantly shorter than its compression (37.1% vs. 62.9%, $P < 0.01$). Posterior dorsal width started to expand at the beginning of the occlusal and peaked at the middle of opening phases, being the only dimensional expansion occurring throughout the occlusal phase. Expansions of LENG and THICK started at the late occlusal, lasted through entire opening and peaked at the middle or late of closing phases (Fig. 6). Quantitative timing analyses also revealed that neither did onsets nor durations of LENG and THICK show significant difference between the working and balancing sides. However, significantly different onsets were seen among the three widths (AW, PVW and PDW, $P < 0.05$ – 0.01). Analyses of magnitudes of these dimensional changes further indicate that expansions of AW and THICK were significantly larger than those of LENG, PDW and PVW ($P < 0.05$ – 0.01). However, LENG and THICK showed no differences between working and balancing sides (Fig. 7).

Even though the two-phased jaw opening occurred, the overall pattern of tongue dimensional changes in relation to jaw movement during ingestion was similar to that during chewing except for AW, which started to expand at the late closing phase (Fig. 8), rather than at the early or middle of occlusal phase (Fig. 6). The expansions of LENG and THICK lasted through almost the entire period of two opening phases and peaked at the early closing phase, indicating that anterior widening, body lengthening and posterior thickening were the major deformational form of the tongue for ingestion (Fig. 8).

The timing relationships of the three widths (AW, PDW and PVW) and their relation to LENG and THICK during drinking were similar to those during chewing with the following exceptions: (i) AW expanded right before jaw opening and peaked at the very late opening phase; (ii) the durations of expansions in both PVW and PDW were significantly shorter ($P < 0.01$) than those during chewing and ingestion; and (iii) unlike chewing and ingestion, the duration of LENG expansion was significantly shorter than that of THICK (43.4% vs. 58.6%, $P < 0.01$, Fig. 9).

Tongue dimensional changes relative to muscle activity

There were no coincident onsets or offsets between muscle activity and dimensional expansion or compression of the tongue. Furthermore, no tongue muscle activity occurred when AW started to expand in the middle of occlusal phase (Fig. 6). Temporally, the first activity bursts of SG, SL and IL were mostly overlapping with the expansion of AW and the late expansion of PDW, whereas their second bursts with the late expansions of LENG and THICK. On the other hand, one-phased activity of GG and V/T was mainly overlapping with the expansions of LENG and THICK (Fig. 6).

No two-phased EMG firing pattern was identified during ingestion. Electromyography of tongue muscles was negligible when all width expansions (AW, PVW and PDW) occurred in the late closing through occlusal phases and all tongue muscles showed similar timing pattern similar to those of LENG and THICK expansions (Fig. 8).

Similar to those found during chewing and ingestion, no EMG activity of the tongue muscles coincided with the time points when tongue widths (AW, PVW and PDW) started to expand. Although more overlapping of EMG activity bursts with the tongue dimensional expansions was seen when compared with those during chewing and ingestion, in particular IL and V/T activity bursts versus AW and LENG expansions, the durations of PVW and PDW expansions showed no overlapping with SG and IL and a little overlapping with GG (Fig. 9).

Quantitative associations between tongue deformation and muscle activity

The correlation analyses between the magnitudes of dimensional changes and IEMG values during chewing indicate that changes in the three widths were significantly associated with IEMG of GG ($P < 0.01$), positively for AW but negatively for PDW and PVW. Anterior width was also significantly associated with IEMGs of the two jaw muscles (MA and DI). In addition, larger changes in AW and PDW were significantly associated with the larger activities of SL and V/T respectively ($P < 0.01$). There was no significant association between the magnitudes of LENG/THICK and IEMG. The only exception is the thickness of working side (W-THICK), which showed a significant and positive association with IEMG of IL ($P < 0.01$, Table 2, top panel).

Very strong positive associations of the magnitudes of dimensional changes and IEMGs were found during ingestion, particularly with all three intrinsic tongue muscles (SL, IL and V/T) and GG (all $P < 0.01$). The only exception was PDW with SL, which exhibited a negative association. While all magnitudes of dimensional changes presented no significant association with IEMG of SG, some of them significantly associated with IEMGs of MA and DI (Table 2, middle panel).

Significant associations between the magnitudes of tongue dimensional changes and IEMGs were fewer during drinking than ingestion. Anterior width and PDW showed an opposite association with IEMGs of SG and MA significantly, positive for AW and negative for PDW ($P < 0.01$), which are the only significant associations of SG with the tongue deformation during three feeding behaviours. A larger lengthening (LENG) was associated with larger activities in GG and V/T ($P < 0.05$ – 0.01), and a larger thickening (THICK) with larger activities in all muscles (GG, SG, IL, V/T and MA, $P < 0.05$), except for unavailable data for DI and SL (Table 2, lower panel).

Discussion

Approaches and limitations

The tongue moves and changes its shape in non-linear directions with a constant volume (1). From this point of view, tongue kinematics can be determined only by measuring the displacement of multiple tongue 'landmarks' through the use of small markers implanted within or secured to the tongue (9, 21). The previous ultrasound studies on tongue movement cannot be used to quantify the temporal and spatial relations between the tongue and jaw (22) and measurements of the tongue shape changes from radiographic projection may not accurately reflect movement in one plane (23). In addition, studies exploring tongue deformation using fluoroscopy and implanted metal markers are limited in the spatial resolution achievable and cannot provide actual 3D changes inside the tongue (3, 4). The recent development of non-invasive tagged MRI technology (13, 24) requires sophisticated mechanical modelling and 3D reconstruction, and cannot provide a real-time reading of various dimensions of the tongue. This study attempted to assess functional deformation of the tongue in various dimensions during feeding, and to link them with muscular activity and jaw movement. The novel technology of sonomicrometrics provides a reliable and accurate tool to evaluate tongue internal kinematics temporally and spatially, and the synchronization technology further allows examining the coordinative organization of the tongue internal kinematics, muscle activity and jaw movement in a precisely real-time manner. Furthermore, jaw movement tracking before and after the crystal implantation further excludes a visible functional interference with the crystal implantation. However, there are two major limitations of the sonomicrometric technique: 1) due to the invasive nature, it cannot be applied for human tongue study; and 2) only linear distance change between a pair of crystals can be measured, thus tongue bending, tipping and twisting cannot be directly assessed.

Although anatomical differences exist, the pig is an ideal animal model to study feeding physiology due to the most similarity in feeding apparatus and function (omnivorous ancestral diet, bunodont and low-cusp dentition, vertical occlusal orientation and isognathic occlusion) to that of higher primates (25). In this study, ten pigs were used and a large amount of feeding cycles (chewing, ingestion and drinking) were analysed. However, successful records (pigs/cycles) were rather limited (see sample sizes in Tables 1 and 2). This pitfall was caused by the following reasons: (i) not all six implanted crystals were operational during certain recordings, which limited available signals; (ii) the system allows only 4-ch output of analogue signals, which further limited available signals; (iii) similarly, not all inserted EMG electrodes were working in some animals; and (iv) any data which were not appropriately synchronized from the three sources (sonomicrometrics, EMG and jaw movement) were excluded. The limitation of this study also exists in the approach to assess the time relationships of the three sources. Although the inherent problem of different sampling rates was overcome by synchronization, the coordinative patterns of these time-dependent variables, i.e. their spatial and temporal connectivity, were only assessed through the identification of a single point of these wave signals, such as the peak value of dimensional changes, onset or offset of EMG activity and starting point of a jaw movement phase. Therefore, certain experimental bias and/or measurement error could confound the results to some extent. Further extraction of these data by the application of time-series analysis may be helpful to overcome these disadvantages (6, 26).

Tongue-jaw linkage in feeding

Although a number of studies have indicated a strong linkage between the tongue and jaw movements during feeding (9, 23, 27), the linkage between the tongue internal kinematics and jaw movement is unknown. This study reveals that the tongue body lengthens and

thickens during food preparatory stage (opening and closing phases), and widens during food crushing/grinding stage (occlusal). The extension of width expansions (AW and PDW) from the occlusal to the early opening phases may imply that, when jaw opens during chewing, tongue body lengthening accompanies with its posterior thickening, dorsal widening and ventral narrowing (Fig. 6). The similar magnitudes of LENG and THICK between the working and balancing sides may further suggest that the tongue may entirely tip over the working side to place food onto the occlusal table of post-canine cheek teeth (7), during which the three longitudinal tongue muscles (SG, SL and IL) of the tipping side (balancing side) may be involved more (15). It is also worthy to mention that changes in the three widths were strikingly different in both timings and amplitudes. Posterior ventral width expanded first at the late jaw closing, followed by those of PDW and AW. Of the three widths, the magnitude of AW expansion was the largest but its duration was the shortest. On the contrary, the magnitude of PDW was moderate, but its duration was the longest (Figs 6 and 7). These features demonstrate that the anterior tongue continues to widen during early jaw opening to prevent food leaking from the mouth, whereas the posterior tongue widens during the occlusal phase to push food against palate, a tongue kinematics pattern similar to that of humans (28). The continuous AW and PDW widening with PVW narrowing during the early jaw opening may help to curve the tongue dorsal surface to hold and/or transfer food for the next crushing/grinding cycle effectively. These timing and magnitude relationships indicate the features of temporal sequence of tongue dimensional expansions in the transverse (AW, PDW and PVW) and sagittal (LENG and THICK) planes of the tongue during chewing.

The reversals from tongue shortening to lengthening and thinning to thickening were not coincident with the initiation of jaw opening, but occurred right before jaw opening (Fig. 6). Given that simultaneous lengthening and widening are the two major components of tongue protrusion, the above relationship may challenge the widely accepted notion that the initiation of tongue protrusion coincides with jaw opening during chewing (9, 23, 27, 29). This asynchronous widening and lengthening of the tongue in relation to jaw opening may suggest that the tongue deforms in shape in a sequential manner while displaces bodily in position, and a regional widening may not be concomitant with lengthening when jaw opens. The presentation of simultaneous lengthening and thickening of the recorded region also suggests that the hydrostat theory may be only applicable for the entire tongue, because this theory requires elongation and shortening being compensated by simultaneous thinning and thickening respectively to keep the volume constant (1). Because changes measured for the length (anterior 2/3) and thickness (junction of anterior 2/3 and posterior 1/3) are not from the same region, the regional variation may also cause this discrepancy. Such a simultaneous increase in the body length and posterior thickness during chewing may further imply that a thickening posterior tongue provides a supporting platform on which tongue body lengthening reaches the peak during late jaw closing. This phenomenon also proves our previous findings that tongue volume does alter regionally during function (6).

Jaw movement and tongue deformation during ingestion have not been well studied. Unlike cats and rabbits (9, 30, 31), the distinction between chewing and ingestion sequences is clear in pigs, and the ingestion episode undergoes stereotypical cycles of jaw movement and tongue deformation with as much as 100% faster rate when compared with that of chewing (15, 16). The featured two-phased jaw opening resembles the slow and fast jaw opening stages when a cat intakes food (30). Simultaneous lengthening and thickening of the tongue body were again seen during ingestion, but occurred at the early jaw opening, rather than the late occlusal phase as seen during chewing (compare Figs 6 and 8). This feature may allow the tongue to protrude out of the mouth to pick up food during ingestion. On the other hand, AW and PVW widens right before the occlusal phase to 'deposit' food in the posterior mouth and to form a bite (32).

A few studies have described jaw movements during natural drinking (33–36). Similar to the other studies, the gape of jaw opening during drinking was much smaller when compared with chewing and ingestion (Table 1). However, jaw movements showed more regular and stereotypical in current young pigs than in infant pigs (36), presenting the consequence of a maturing neuromuscular circuit and motor learning process. The tongue internal kinematic during drinking was for the first time described in our previous study (16). This study further reveals that the anterior widening (AW) and body lengthening (LENG) occurred along with jaw opening, whereas posterior thickening (THICK) lasted from the early opening through late closing (Fig. 9). This specific pattern of dimensional changes suggests that the tongue stretches in width first before jaw opening, then elongates and thickens to form a central groove during drinking. This is an ideal shape to exert the mechanism of suction, because no lapping and licking for liquid feeding is reported in pigs and most of ungulates (16, 36, 37).

Tongue deformation and muscle activity

Traditionally, regional changes in tongue shape (deformation) are thought to be produced by the activity of the intrinsic tongue muscles and larger changes in space (movement) by the extrinsic tongue muscles, because the architecture and behaviour constraints limit the contribution of extrinsic muscle to localized change of tongue shape (38). However, extensive studies have demonstrated that although some tongue regions are controlled by the intrinsic muscles independently in mammals, both the intrinsic and extrinsic muscle groups interweave and act in concert with each other in most functional activity (2, 6, 15, 39, 40). In most cases, tongue movement and deformation cannot be distinguished from each other because the tongue is a constant volume structure and its movement is produced by change in shape (1, 41).

To the best of our knowledge, no study has addressed the question how the activity of tongue (and jaw) muscles relates to tongue internal kinematics. This study provides the evidence that the co-activation of multiple muscles, both the intrinsic and extrinsic, is common during tongue internal deformation. However, these deformations do not always couple with muscle activities in timing. Moreover, the widening of anterior and posterior tongue even started and proceeded during the silent period of the tongue muscle activity in all three feedings (Figs 6, 8 and 9). Therefore, it is reasonably assumed that the reversals between the dimensional expansion and compression of the tongue are not initiated or driven by the tongue muscle contractions and the passive stretching of jaw movement may play a major role on these reversals. This assumption can be supported by the fact that most of these reversals occurred in the duration of MA activity (Figs 6, 8 and 9) and the fact that jaw muscle activities were significantly associated with dimensional changes, in particular with the tongue widening (Table 2).

According to the locations and fibre orientations, GG and V/T are recognized as ‘structural unit’ of the inner musculature, whereas SG, SL and IL are classified as the outside cover or fringe of the tongue (42, 43). Overall, the EMG activity of the inner structural unit (GG and V/T) overlapped more with the dimensional changes (lengthening/posterior thickening, LENG and THICK) than that of the cover/fringe (SG, SL and IL) during all three feedings. It should be noted that although IEMGs of SG, SL and IL presented higher amplitudes in the balancing than working sides during chewing (15), LENG and THICK changes showed no significant difference between the two sides (Fig. 7). This feature suggests that tongue sagittal deformation may not be closely related to the activity of tongue longitudinal muscles (SG, SL and IL). In fact, significant associations between sagittal deformations of the tongue and longitudinal tongue muscle activities were only found between THICK and IL in the working side. On contrast, transverse deformations (AW, PDW and PVW) seemed to have more significant associations with the tongue muscle activities (Table 2).

Unlike chewing, all five dimensional changes during ingestion showed significant associations with activities of three intrinsic muscles (SL, IL and V/T) except for PDW with IL (Table 2). This striking difference may be due to the fact that both transverse (widening) and sagittal (lengthening and thickening) deformations are predominant during ingestion (16). While AW and PVW were positively associated with all intrinsic tongue muscles except for SG, PDW showed a negative or no association with the two longitudinal muscles (SL and IL). This fact implies that a stronger activity of SL and IL may result in an opposite direction of the posterior widening in the ventral and dorsal regions during ingestion. As for the extrinsic muscles, only GG showed a strong positive association with LENG and THICK during ingestion. Therefore, the intrinsic tongue muscles and GG might play the major role for ingestion because the tongue lengthening and thickening are mainly seen within the activation periods of these muscles (Fig. 8). These associations further suggests that SG, a major tongue retractor muscle, may have less contribution to the tongue internal deformation, because no association with any of dimensional changes was identified during both chewing and ingestion (Table 2). On the other hand, the linear mechanical effect of the muscle contraction on altering tongue shape is more apparent during ingestion than chewing and drinking because there were more and stronger positive associations between AW/THICK and muscle activities (Table 2).

Strikingly different from chewing and ingestion, both SG and MA showed strong associations with tongue widening and thickening, positive for AW and THICK and negative for PDW. We previously demonstrated the functional connectivity or temporal coupling between MA and SG in mastication (9), this study further suggests that this relationship between MA and SG may be more apparent for drinking than for chewing and ingestion. Furthermore, because there is no significant association between tongue widening (AW, PDW and PVW) and the activities of IL and V/T, the tongue intrinsic muscles may contribute less to the deformations in the transverse (AW, PDW and PVW) than sagittal (LENG and THICK) planes during drinking.

There were several opposite associations between tongue deformations and muscle activities (positive vs. negative, Table 2), indicating that the same level of contraction in a specific muscle may produce an opposite mechanical effects on individual dimensional changes. For example, larger activity of GG may result in more widening in the anterior (AW) than the posterior (PDW and PVW) during chewing (Table 2, upper panel), as seen between SL/SG activities and tongue widening during ingestion and drinking (Table 2, middle and lower panels). Interestingly, these opposite associations were only related to transverse (widening), rather than sagittal (lengthening and thickening) deformations. This feature is consistent with their temporal relationships, i.e. the sagittal deformations of the tongue are better coupled with the tongue muscle activities than do the transverse deformations (Figs 6, 8 and 9).

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Fig. 1. Schematic diagram of the sonomicrometric crystal array (small empty circles and numbers) and jaw movement markers (large solid circles). Hatched area presents the tongue and dashed lines indicate upper and lower segments of jaw movement. L and R: left and right. 1–2: anterior width (AW); #3–4: posterior dorsal width (PDW); #5–6: posterior ventral width (PVW); #1–3 and #2–4: right and left lengths (RL and LL, or LENG); #3–5 and #4–6: right and left posterior thicknesses (RT and LT or THICK).

Fig. 2.

Raw tracings of jaw movement trajectory and electromyo-graphic activity (EMG) of masseter (MA). A: chewing, R and L indicate chewing side; B: ingestion; C: drinking; O: opening phase; C: closing phase; OP: occlusal phase. O₁ and O₂: the first and second opening phase; RMA and LMA: right and left masseters.

Fig. 3.

Raw electromyography (EMG) and sonomicrometric tracings during chewing. R and L above the tracings indicate the chewing side. RMA: right masseter; RDI: right digastrics; RGG: right genioglossus; RSG: right styloglossus; RV/T: right verticalis/transeversus; RSL: right superior longitudinalis; RIL: right inferior longitudinalis; AW: anterior width; RL: right length; PDW and PVW: posterior dorsal and ventral widths.

Fig. 4.

Raw EMG and sonomicrometric tracings during ingestion. RMA: right masseter; RDI: right digastrics; RGG: right genioglossus; RSG: right styloglossus; RV/T: right verticalis/transeversus; RSL: right superior longitudinalis; RIL: right inferior longitudinalis; AW: anterior width; RL: right length; PDW and PVW: posterior dorsal and ventral widths.

Fig. 5. Raw EMG and sonomicrometric tracings during drinking. RMA: right masseter; RDI: right digastrics; RGG: right genioglossus; RSG: right styloglossus; RV/T: right verticalis/transeversus; RSL: right superior longitudinalis; AW: anterior width; RL: right length; PDW and PVW: posterior dorsal and ventral widths. Arrows indicate swallowing episodes.

Fig. 6.

Time sequences (onsets and offsets) and durations of tongue dimensional changes and EMG in relation to the phases of jaw movement during chewing. All values were converted to the proportion (%) of chewing frequency (total cycle length, 100%). Jaw: jaw movement; OP: occlusal phase, O: opening phase; C: closing phase; RMA: right masseter; DI: right digastrics; GG: right genioglossus; SG: right styloglossus; SL: right superior longitudinalis; IL: right inferior longitudinalis; V/T: right verticalis/transeversus; AW: anterior width; PDW and PVW: posterior dorsal and ventral widths; THICK: right posterior thickness; LENG: right length. Left and right lines in each bar indicate s.d. for onsets and durations respectively. Filled bars indicate the EMG bursts (EMG) and the tongue dimensional expansions (Sono) and empty bars indicate the EMG silent period and (EMG) and the tongue dimensional compression (Sono).

Fig. 7.

Comparisons of the magnitudes of the tongue dimensional changes during chewing. All values were converted to % of the initial distance of a given crystal pair measured at the implantation. Asterisks indicate significant differences between dimensions. AW: anterior width; PDW and PVW: posterior dorsal and ventral widths; LENG: right length, THICK: right posterior thickness. * $P < 0.05$; ** $P < 0.01$.

Fig. 8.

Time sequences (onsets and offsets) durations of tongue dimensional changes and EMG activities in relation to the phases of jaw movement during ingestion. All values were converted to the proportion (%) of ingestion frequency (total cycle length, 100%). Refer to Figs 2, 3 and 6 for other captions. Jaw: jaw movement; OP: occlusal phase, O₁ and O₂: the first and second opening phase; C: closing phase; RMA: right masseter; DI: right digastrics; GG: right genioglossus; SG: right styloglossus; SL: right superior longitudinalis; IL: right inferior longitudinalis; V/T: right verticalis/transeversus; AW: anterior width; PDW and PVW: posterior dorsal and ventral widths; THICK: right posterior thickness; LENG: right length. Left and right lines in each bar indicate s.d. for onsets and durations respectively. Filled bars indicate the EMG bursts and the tongue dimensional expansions, and empty bars indicate the EMG silent period and the tongue dimensional compression.

Fig. 9.

Time sequences (onsets) and durations of tongue dimensional expansions and EMG activity in relation to the phases of jaw movement during drinking. All values were converted to the proportion (%) of drinking frequency (total cycle length, 100%). Jaw: jaw movement; OP: occlusal phase, O: opening phase; C: closing phase; RMA: right masseter; DI: right digastrics; GG: right genioglossus; SG: right styloglossus; IL: right inferior longitudinalis; V/T: right verticalis/transeversus; AW: anterior width; PDW and PVW: posterior dorsal and ventral widths; THICK: right posterior thickness; LENG: right length. Filled bars indicate the EMG bursts and the tongue dimensional expansions and empty bars indicate the EMG silent period and the tongue dimensional compression.

Table 1

Characteristics of jaw movements

	Chewing (9/139)		Ingestion (8/155)		Drinking (2/41)	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
Rate (ms)	396	59	244*	42	445	58
Gape (°)	13.9	2.5	10.8*	4.5	5.3**	1.8
Phases (%)						
Opening 1	30.4	5.5	33.0	4.3	48.0**	9.7
Opening 2	–	–	19.8	3.6	–	–
Closing	24.5	2.9	25.6	4.2	37.0*	11.0
Occlusal	45.1	5.0	21.6**	7.1	15.0**	2.5

Numbers in parentheses indicate animal and cycle numbers.

Phases are represented as % of rate of jaw movement.

* $P < 0.05$

** $P < 0.01$ compared with chewing.

Table 2

Correlations between tongue deformation and electromyographic activity

	MA	DI	GG	SG	SL	IL	V/T
Chewing (25–74)							
AW	0.386 *	0.449 **	0.407 **	0.041	-0.011	0.027	0.489 **
PDW	0.114	-0.105	-0.398 **	0.027	0.409 **	-0.033	-0.092
PVW	0.018	0.059	-0.478 **	-0.181	0.262	-0.180	-0.051
W-LENG	0.080	-0.038	-0.002	-0.097	0.130	0.090	0.066
B-LENG	-0.073	0.118	0.086	-0.205	0.185	0.024	0.157
W-THICK	0.319	0.365	0.014	-0.249	0.115	0.461 **	-0.018
B-THICK	-0.213	0.215	0.132	-0.218	-0.162	0.242	-0.153
Ingestion (32–105)							
AW	0.374 **	0.311 **	0.323 **	0.202	0.421 **	0.352 **	0.335 **
PDW	0.267	-0.044	0.212	-0.164	-0.439 **	0.205	0.576 **
PVW	-0.232	0.723 **	0.376 **	-0.008	0.473 **	0.455 **	0.516 **
LENG	0.020	0.256	0.539 **	0.270	0.556 **	0.474 **	0.744 **
THICK	0.455 **	0.796 **	0.682 **	-0.111	0.586 **	0.528 **	0.569 **
Drinking (11–32)							
AW	0.661 **	-0.067	0.175	0.510 *	n/a	-0.332	-0.322
PDW	-0.434 *	-0.168	-0.041	-0.501 *	n/a	0.194	0.402
PVW	-0.249	-0.223	-0.029	0.238	n/a	-0.020	0.234
LENG	0.179	0.056	0.616 **	0.182	n/a	-0.263	0.409 *
THICK	0.477 *	n/a	0.487 *	0.736 *	n/a	0.682 *	0.536 *

W, working side; B, balancing side; AW, anterior width; PDW, posterior dorsal width; PVW, posterior ventral width; LENG, length; THICK, thickness; SL, superior longitudinalis; IL, inferior longitudinalis; V/T, verticalis/transversus; GG, genioglossus; SG, styloglossus; MA, masseter; DI, digastricus; n/a, not applicable.

Numbers in parentheses indicate the ranges of sample size (cycle numbers).

Bold values indicate statistically significant coefficients.

* $P < 0.05$

$P < 0.001$
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