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SYMPOSIUM ARTICLE

Regional Heterogeneity in the Electromyography Activity of Extrinsic Tongue Muscles Is Critical to Tongue Function

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Synopsis The tongue, as a muscular hydrostat, performs several dynamic behaviors and functions, including feeding, vocalizing, and respiration. As such, this hydrostat must be capable of performing complex movements, which are powered via a set of muscles typically defined as "extrinsic" (originating outside of the tongue) and "intrinsic" (contained wholly in the tongue). These muscles are typically classified based on their gross anatomical positions and also are often ascribed functions based on these positions, with the extrinsic muscles being assigned the role of positioning the tongue, and the intrinsic muscles thought to function to shape it. For example, genioglossus is typically described as a tongue protruder, whereas hyoglossus is often described as a tongue retractor. However, the neural control of these muscles involves relatively small motor units, and defining the function of tongue muscles based on anatomy, when they occupy overlapping space and exhibit refined control may over-simplify their function. Yet, distinguishing between gross anatomical structures and refined neural control can be challenging due to the complexity of functions the tongue performs. Here, we used an infant animal model (pigs) to evaluate how the neural control of the tongue is modulated in anatomical space given a relatively simplified behavior (suckling). We tested for variation in control along the anteroposterior and dorsoventral axis of the tongue using high speed videofluoroscopy coupled with electromyography (EMG). We found variation in EMG firing timing along both axes, which correspond to differences in behaviors. Furthermore, this variation in activity is likely reflected by regional variation in function within a muscle. These data suggest that defining muscles by their anatomical structure over-simplifies their functional roles and that studies investigating the three-dimensional structure and function of the tongue should evaluate it based on regional variation in control, in the context of the behavior of interest.

Introduction

The mammalian tongue functions in several critical behaviors, including breathing, vocalization, and feeding (Hiiemae and Crompton 1985; Hiiemae and Palmer 2003; Jugé et al. 2023; Ludlow 2011). As a muscular hydrostat, the tongue can deform in three dimensions, and the muscles within it act to both support and generate movement (Kier and Smith 1985). Because of the importance of the tongue in several critical biological functions, understanding its movements and control has been an active area of study in both biomedical and basic science research (Cullins and Connor 2024; Schwenk 1995; Smith 1986). As such, we have a well-developed understanding of the overall anatomy of the tongue. Historically, the muscles that control this hydrostat have been defined as extrinsic, which are the muscles that originate on structures outside the tongue itself (i.e., the hyoid bone for hyoglossus), and then insert in the tongue, or intrinsic, which are the muscles that both originate and insert into the tongue itself (Gray 1918). As a result of these different anatomical arrangements, the extrinsic musculature is typically characterized as controlling the position of the tongue, whereas the intrinsic musculature is often described as controlling the shape of the tongue (Hiiemae and Palmer 2003; Kayalioglu et al. 2007).

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These anatomical definitions have led to several bodies of work extrapolating on the functioning of the tongue. Genioglossus, which originates on the genial process of the mandible and inserts into the tongue dorsally and posteriorly, is often described as protruding the tongue (McClung and Goldberg 2000; Thexton et al. 1998). In contrast, hyoglossus, another extrinsic muscle, is often assigned the function of retracting the tongue while also depressing its lateral margins (Iskander and Sanders 2003; Orsbon et al. 2020; Steer et al. 2023). These functions are typified in experimental work, and have been used in several modelling studies examining how the tongue might be controlled, as well as even the development of soft robots (Hermant et al. 2017; Ishikawa et al. 2025; Stavness et al. 2012). While this work has made important advances in understanding potential roles of this muscular hydrostat, they often fail to recognize that the motor units controlling these structures are relatively small and that the tongue is built more for precision than to achieve large amounts of movement (Mu and Sanders 1999; Mu and Sanders 1999; Mu and Sanders 2000). Furthermore, several recent studies have demonstrated that the delineation of function between and within muscles is an oversimplification, and that the extrinsic and intrinsic muscles act together in most activities (Kayalioglu et al. 2007; Liu et al. 2008; Liu et al. 2009).

In addition to these challenges, the tongue functions in many behaviors, often simultaneously. For example, the anterior portion of the tongue may be involved in food acquisition or processing, while at the same time the posterior regions of the tongue may be powering swallowing (Hiiemae and Crompton 1985; Mayerl et al. 2020; Thexton et al. 1998; Thexton et al. 2007). Thus, there is a high potential that the same muscle may be contributing to two separate behaviors, and exhibiting two separate functions, that vary by both anatomical region and neural control. This is especially critical given the anatomy of the tongue, which does not operate over defined joints as many of the masticatory or locomotor muscles do. As a result, it has been suggested that a more practical way to delineate variation in tongue function would be to use distinctions in neural control or employ functional regions as the unit of analysis, rather than define the anatomy of the tongue by externally visible structures (Schwenk 2001a; Schwenk 2001b), and even within a single muscle several functional units are likely to exist (Wrench 2024).

However, understanding how these "functional regions" may be operating in the neuromotor control of the tongue during feeding can be challenging because of the many behaviors and functions in which the tongue plays a role in. For example, even within feeding, the tongue is involved in acquiring food, manipulating it and transporting it prior to swallowing, in addition to interacting with the teeth during mastication (Feilich et al. 2021; Hiiemae and Crompton 1985; Laurence-Chasen et al. 2023). To explicitly evaluate how variation in neural control is related to function, cyclic behaviors that are dependent primarily on the tongue, with minimal expected variation, should be examined. One such behavior is suckling in infant mammals (Mayerl et al. 2020; Thexton et al. 2004). Suckling requires the tongue to latch onto a nipple, form a seal around it, and then use movements of the tongue to generate suction in the oral cavity, extract milk from a nipple, transport it, and then swallow it (German et al. 1992; Mayerl and German 2023; Mayerl et al. 2024). To accomplish this, the tongue is depressed in an anteroposterior wave as the seal along the dorsum of the mouth translates posteriorly to increase oral volume and generate suction (Cannon et al. 2016; Mayerl et al. 2022; Steer et al. 2023). Unlike in adult feeding, there is no oral processing and milk is essentially moved linearly from the nipple to the back of the oropharynx where it is accumulated and swallowed. Similarly, suckling is controlled by a central pattern generator, and as long as environmental conditions (i.e., milk flow, temperature, nipple properties) remain constant, is a stereotyped process (German et al. 1997; Mayerl et al. 2019). Any variation in neural control within the tongue is therefore reflective of variation of control and function, rather than due to responses to external sensations that would occur during food manipulation and the shifts between balancing side teeth during mastication. This makes suckling an ideal model for testing for different functional roles across subregions of individual muscles.

Here, we used a validated infant animal model, pigs, to evaluate how the neuromotor control of the muscles typically referred to as extrinsic muscles of the tongue varies across the anatomical axis of the muscle during suckling. We hypothesize that the functional regions of the extrinsic tongue muscles are best distinguished by control via different motor units. Therefore, we expect to see high levels of regional heterogeneity in electromyography (EMG) activity across these axes, likely correlated to how the muscles are working to facilitate different behaviors.

Methods

Animal care and husbandry

All animal care and surgical procedures were approved by NAU IACUC #22–010. We purchased infant pigs ($N = 3$, Pig 13, male; Pig 14, female; Pig 16, female) at 24 hours of age from Premier Biosource (Yorkshire/Landrace cross). Infants were trained to feed on a custom bottle-nipple designed to mimic breastfeeding in pigs (similar to Mayerl et al. 2024), and fed milk replacer (Ralco Birthright, Marshall, MN, USA).

Surgical procedure

At approximately 13 days of age, we performed a sterile surgery in which a midline incision was made at the neck. We used a 20-gauge needle to place eight fine-wire bipolar electrodes in muscles of interest. Each electrode was secured individually to soft tissue, and then all electrodes were bundled, and secured together to soft tissue with suture, and then exited the incision at its posterior end. Electrodes were constructed by soldering eight individual wires to an 8-pin microconnector, and then electrode pairs were wound together and loaded into needles, with one wire shorter than the other.

We inserted six electrodes into genioglossus, and two into hyoglossus. Genioglossus was identified by making a small window at the margins between the anterior and posterior portions of mylohyoid (Mayerl et al. 2022), and then parting the two bellies of geniohyoid until genioglossus could be identified. To insert electrodes, we placed one electrode in the ventral portion of the left belly of the muscle at its anterior margin, and another at the same anteroposterior position, but one cm deeper into the muscle. We repeated these two insertions at the midbelly of genioglossus, and at its posterior margin (Fig. 1). We identified hyoglossus by creating a small window in the posterior margin of mylohyoid lateral to the midline using blunt dissection. Hyoglossus was identified as being between the posterolateral margin of geniohyoid and deep to mylohyoid, diving dorsally into the tongue. We placed one electrode anteriorly in the belly, and one electrode posteriorly, close to the insertion on the hyoid bone, with surgical placement confirmed via diffusible iodine-based contrast-enhanced computed tomography (diceCT) after euthanasia (Gignac et al. 2016; Mayerl et al. 2021b; Mayerl et al. 2021c; Mayerl et al. 2022). We have had consistent success in precision placement of electrodes over many surgeries, confirmed post-mortem (Mayerl et al. 2021b; Mayerl et al. 2021c; Mayerl et al. 2022). We placed a ground posterior to the ear, with a plug extending out of the incision to reduce electrical noise. The 8-pin microconnector was then connected to an "interneuron," that had an 8-pin microconnector on one end and an ethernet plug on a distal end that was connected to the amplifier during data connection. Connections were waterproofed and the interneuron was secured to the body with self-adhesive bandage wrap and tubular bandage to ensure that wires were not pulled out by the animal during recovery.

Data collection and processing

We synchronously collected high-speed (100 fps, 12 MP Redwood, IO industries, Ontario, Canada) biplanar videofluoroscopic video (82–102 kV, 5.2–8.0 mA) with EMG data during feeding using a 16 channel Powerlab and amplifier (16/35, ADInstruments, Colorado Springs, CO, USA), with intraoral pressure generation using a Milar pressure catheter threaded through the tip of the nipple and into the infants mouth in one feeding session per individual (Mayerl et al. 2021d; Steer et al. 2024). We collected and analyzed 81 sucks, and 48 swallows across the three individuals (Pig 13: 28 sucks, 12 swallows; Pig 14: 28 sucks, 14 swallow; Pig 16: 28 sucks, 22 swallows).

Data processing

Pressure data were integrated with a rolling median to 100 Hz to match X-ray video. Sucks were identified as beginning at the time at which suction generation began, and ending 0.01 s prior to the next suction generation minimum, identified and verified by a custom R script. Swallows were identified from X-ray video as the frame at which the bolus was accumulated in the posterior of the oropharynx, prior to posterior movement past the epiglottis, following published protocols (Mayerl et al. 2021a; Mayerl et al. 2021d). EMG data were processed using published protocols in which data were rectified, integrated, and thresholded (Mayerl et al. 2022; Thexton 1996).

Suck identification was combined with EMG data such that the onset of EMG activity was determined relative to the beginning of each suck. Where electrodes showed differential activity between sucks and swallows, or only detected swallows, we removed those electrodes from analyses of sucks, and instead calculated EMG onset of those electrodes relative to the beginning of the swallow (Thexton et al. 2012).

Statistical analyses

Statistical analyses were performed using R (v 4.3.1). Suck duration was fairly invariable (0.277s ± 0.028 s), as in previous work that demonstrated that cycle length is fairly consistent in suckling (Gierbolini-Norat et al. 2014). As such, we compared the onset of muscle timing relative to the beginning of the suck for genioglossus and hyoglossus using linear mixed effects models

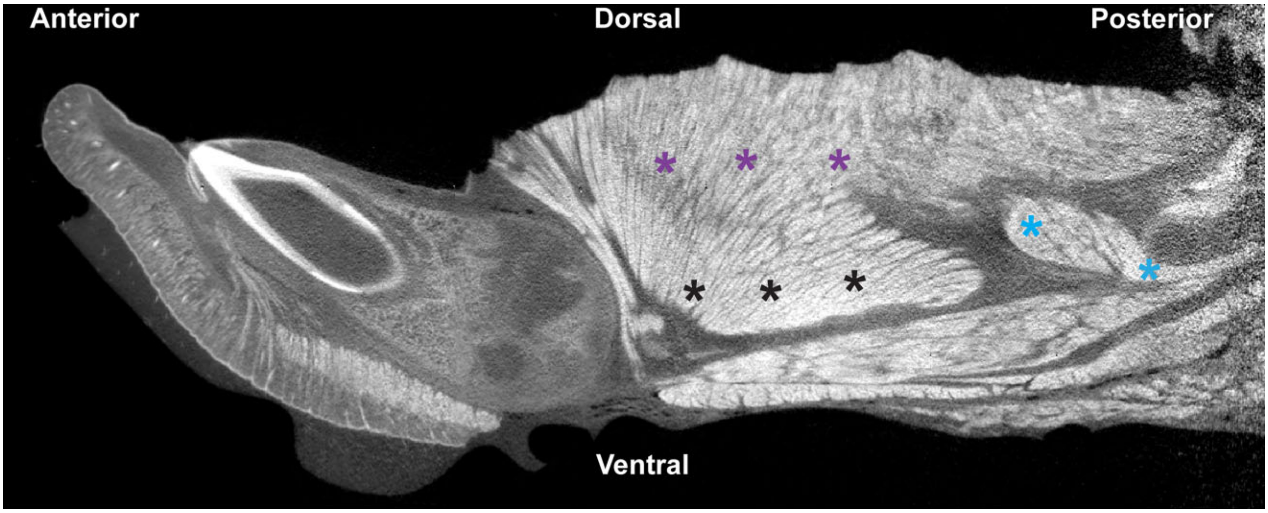

Fig. 1 Sagittal view of a diceCT scan of an infant pig, highlighting electrode placements of hyoglossus (blue asterisks, posterior) and genioglossus in ventral (black) and dorsal (purple, top) placements. Anterior of the pig is on the left, posterior on the right.

(Bates et al. 2015), with dorsoventral and anteroposterior (or just anteroposterior for hyoglossus) position as fixed effects, and individual animals as random effects to account for interindividual variation impacting statistical analyses. Because interaction terms were significant for genioglossus, we performed planned contrast analyses coupled with Cohen's *d* to evaluate differences between anteroposterior and dorsoventral positions explicitly (Cohen 1992; Length et al. 2018). For hyoglossus, we calculated Cohen's *d* in comparing anteroposterior locations (Cohen 1992). Cohen's *d* is a metric of effect size and is considered small if $0.2 < d < 0.5$, medium if $0.5 < d < 0.8$, and large if $0.8 < d$.

Results

Genioglossus timing

We found substantial variation in the onset of genioglossus relative to the beginning of the suck in both dorsoventral and anteroposterior directions (Fig. 2).

Dorsoventral variation in genioglossus timing

Firing timing in the anterior portion of genioglossus did not vary by dorsoventral location. However, in the middle of the tongue, the ventral portion of genioglossus fired earlier than electrodes placed dorsally (Fig. 2, Table S1). Conversely, in the posterior margin of the tongue, the ventral electrode recorded activity later than the dorsal electrode, albeit with only a medium effects size (Fig. 2, Table S1). Furthermore, there was inter-individual variation in which behaviors were detected in the posterior dorsal electrode: in one individual (Pig 13), only sucks were recorded, in another (Pig 16), sucks and swallows were recorded but showed different amplitudes of firing, and in the last individual (Pig 14), only swallows were recorded by the electrode, resulting in this individual being removed for analysis of timing during sucking (Pig 14, Fig. 3). In this individual (Pig 14), the posterior dorsal genioglossus electrode recorded activity slightly after the initiation of the swallow, which differed from onset timing of Pig 16, where electrodes recorded activity close to the initiation of the swallow (Fig. S1).

Anteroposterior variation in genioglossus timing

We found an anteroposterior wave of activity timing in both dorsally and ventrally placed electrodes, where anterior electrodes recorded activity closer to the onset of the suck than electrodes placed in the middle of genioglossus, and both anterior and middle electrodes recorded activity earlier than posteriorly placed electrodes, with medium to large effect sizes (Fig. 2, Table S1).

Anteroposterior variation in hyoglossus timing

Electrodes meant to be placed in hyoglossus were in the posterior belly of mylohyoid in one individual, which was removed from analysis (Pig 16, Mayerl et al. 2022). In the other two individuals, the onset of hyoglossus activity recorded from the anterior electrode occurred shortly after the initiation of the suck (Fig. 4, $t = 1.56$, $P = 0.13$, $D = 0.42$). However, we did find inter-individual variation in whether sucks or swallows were detected in the posterior electrode, as in one individual, only swallows were detected, whereas in the

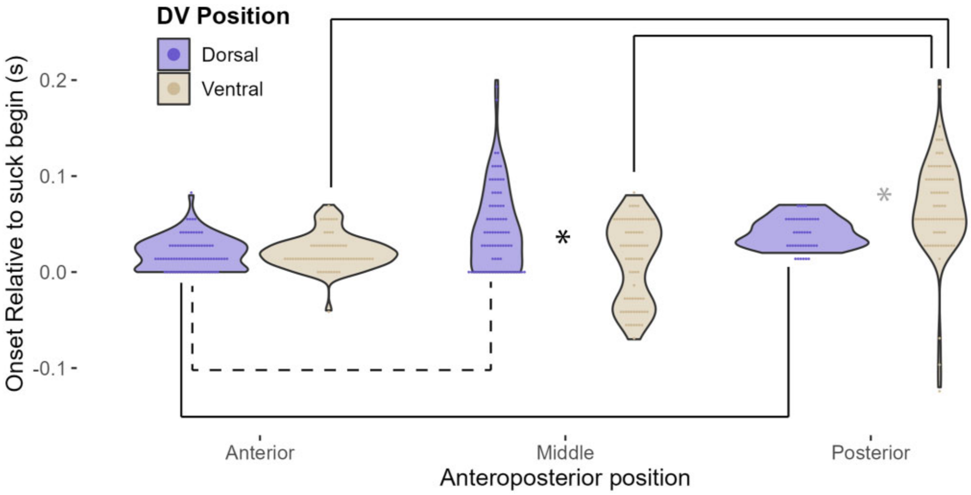

Fig. 2 Violin and dot plot indicating EMG onset timing for genioglossus relative to the beginning of the suck. There was an anteroposterior wave of timing in both dorsal (purple, left) and ventral (beige, right) electrode locations, with some variation dorsoventrally in the middle and posterior positions. Lines indicate statistically significant differences with large (solid, $d > 0.8$) or medium (dashed, $d > 0.5$ and < 0.8) effect sizes depending on anteroposterior position. $*$ indicates statistically significant differences with a large (black) or medium (gray) effect size for dorsoventral position.

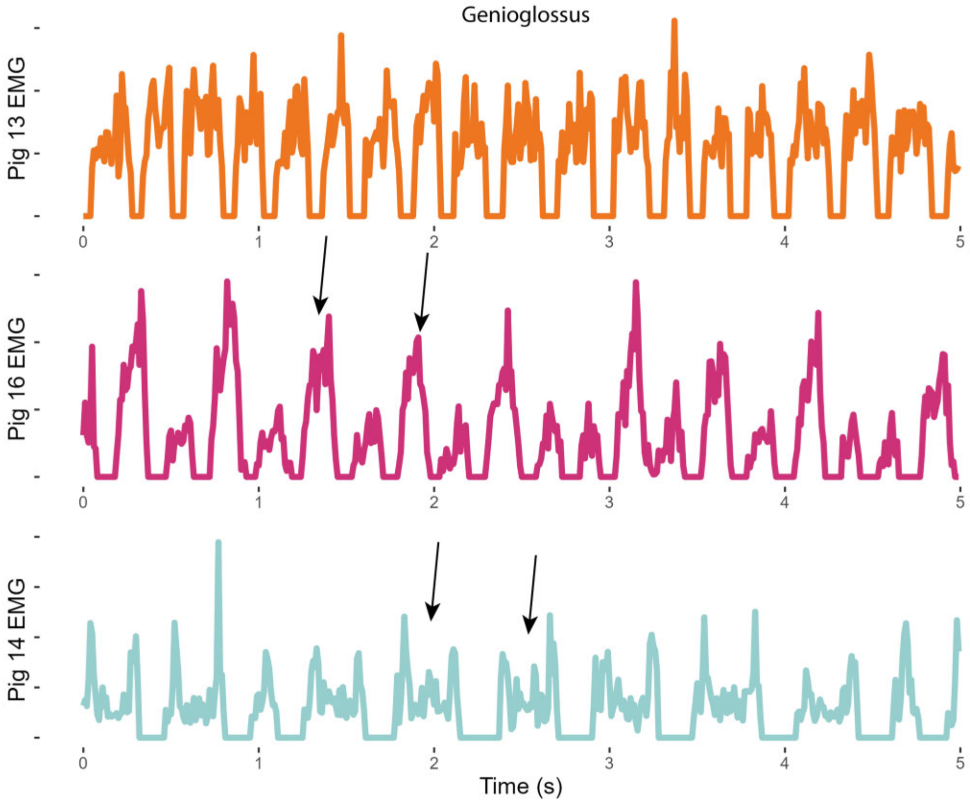

Fig. 3 Representative recording of EMG activity in the posterior dorsal portion of genioglossus across pigs. Electrodes either recorded activity during sucks (Pig 13, orange, top), recorded differential activity during swallows but were also active during sucks (Pig 16, pink, middle), or recorded only swallows (Pig 14, blue, bottom). Example swallow recordings are indicated by the black lines for pigs 16 and 14.

other, only sucks were detected (Fig. S2). In the individual where hyoglossus posterior detected swallows, the muscle turned on shortly before the swallow began (Fig. S1).

Discussion

In many ways, muscles have fundamentally similar construction, with cross bridges, actin, myosin, and titin,

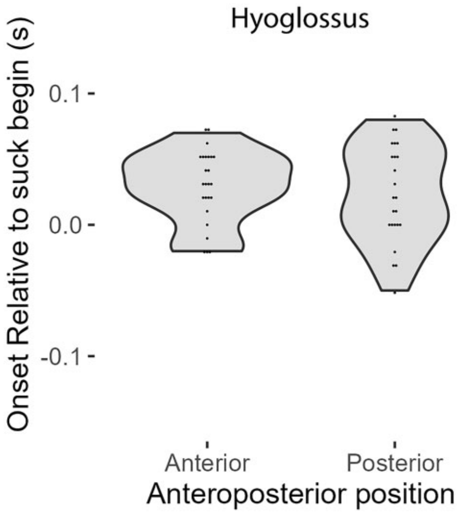

Fig. 4 Violin and dot plot indicating that the onset of hyoglossus EMG activity relative to the beginning of the suck in anterior (left) and posterior (right) electrodes did not differ. The anterior plot contains data from two individuals, whereas the posterior plot only contains data from one.

and intrinsic properties that all work similarly in striated muscle (Nishikawa et al. 2007; Nishikawa et al. 2018). Yet, at the organismal level muscles can function in very different ways: to power (act as a motor), constrain (act as a strut), oppose movement (act as a brake), or some combination of all three (Ahn and Full 2002; Dickinson et al. 2000). Yet even within a muscle, there is important variation in function that is critical for successful performance. The activity of genioglossus and hyoglossus was highly variable depending on electrode location during suckling in infant pigs. We found anteroposterior variation in activity in both muscles, especially related to electrode placement location, as well as variation in activity along the dorsoventral axis of the tongue in genioglossus as the fibers extended from their insertion on the genial process. Electrodes placed posteriorly, especially in hyoglossus and the dorsal portion of genioglossus exhibited variation across individuals. Specifically, their activity varied across behaviors, where recordings from some individuals only consisted of sucks, others recorded sucks and swallows, and others recorded only swallows (note that it is not the swallow that is absent or present, but that the EMG signal from a specific electrode muscle recording). These differences likely stem from variation in exact electrode positioning across individuals and reflect the relatively small motor units in hyoglossus and genioglossus as well as the ability of fine-wire electrodes to record from a small number of units (Cundall and Gans 1979; McClung and Goldberg 2000; Mu and Sanders 2000). Previous work has shown significant differences in firing patterns among electrodes intentionally placed close together (German et al. 2008; German et al. 2009; Thexton et al. 2007). The variation we measure is likely from both experimental technique and inherent variation in neuromuscular anatomy in these small and specifically controlled muscles.

Potential variation in function: anteroposterior axis

The high regional heterogeneity in the anteroposterior axis of both genioglossus and hyoglossus likely are reflected by variation in function across the long axis of the tongue, as well as the relatively small motor unit pools in these muscles (Kayalioglu et al. 2007; Mu and Sanders 2000; Wrench 2024). The anteroposterior wave in genioglossus is likely helping to generate the anteroposterior wave the tongue makes as milk is acquired and then transported to the back of the oral cavity within a single suck (Elad et al. 2014; Haravu et al. 2023). While this wave is specific to the consumption of liquids via suction, we might expect to see similar patterns in mammalian drinking, for example through a straw, but different patterns when exploring other mechanisms of liquid acquisition (i.e., Steer et al. 2023a). Furthermore, while we did not explore the potential for variation within genioglossus across a mediolateral axis, we would expect that in mammals that use extensive oral processing as adults, regional heterogeneity in firing would be similarly related to tongue movements, as well as tongue shape (Feilich et al. 2021; Laurence-Chasen et al. 2023; Olson et al. 2021; Olson et al. 2023; Orsbon et al. 2020; Williams et al. 2007). Thus, in the anteroposterior axis, there can be high levels of functional variation and fine scaled neural control in genioglossus. If the function of genioglossus is defined by its anatomy, as opposed to neural control, this may not represent the muscle's true role in powering the muscular hydrostat of the tongue.

Individual muscles have the potential to exhibit variation in both activity patterns, and in length changes (Azizi and Deslauriers 2014; Holman et al. 2012; Konow et al. 2010; Rahemi et al. 2014; Tijs et al. 2021). In hyoglossus, variation in firing along the anteroposterior axis is likely driven by the role of this muscle in powering both sucking and swallowing. The anterior portion of the muscle, close to where its fibers merge with the rest of the tongue, likely is important in depressing the tongue as well as continuing the anteroposterior wave of tongue movement during suckling. However, anterior contraction does not result in anterior movement of the hyoid during suckling. While other antagonistic muscles likely play a role in maintaining hyoid posture (German et al. 2011), it is possible that regional heterogeneity in firing timing could allow for regional variation in length changes during activity to also exist. This is supported by the fact that many of the hyoid muscles have already been demonstrated to exhibit regional heterogeneity in both firing patterns and length changes during activity, which are associated with different behaviors and different anatomical regions (Holman et al. 2012; Konow et al. 2010; Mayerl et al. 2022). Thus, the regional heterogeneity in firing observed along the anteroposterior axis of hyoglossus could function in controlling behaviors associated with sucking vs. swallowing, which has been suggested by previous work (German et al. 2009; Thexton et al. 2012). If an electrode is posterior enough, the motor units are functioning to exert a concentric contraction and move the hyoid during a swallow. There is, however, a point in hyoglossus posteriorly where the muscle is only active during suckling, and potentially only sarcomeres anterior to that point would be assisting with moving the tongue, while the hyoid is stabilized by antagonistic muscles (Thexton 1984; Thexton et al. 1998; Thexton et al. 2007). We propose that during suckling, hyoglossus functions as a motor to generate work anteriorly and as a brake to absorb it posteriorly, but during swallowing shifts to function as a motor posteriorly to assist with hyoid movement. This needs to be tested by either sonomicrometry or fluoromicrometry in conjunction with EMG. Yet, the high regional heterogeneity in hyoglossus, as in genioglossus, suggests that the description of this muscle by anatomy, rather than motor activity, does not adequately delineate its function.

Potential variation in function: dorsoventral axis

We also found substantial variation in the dorsoventral axis of genioglossus, although the extent of this varied. For example, there was no variation in EMG timing between dorsal and ventral electrodes in the anterior portion of the tongue. This aligns with the role of the anterior tongue during suckling: the tongue must latch on to the nipple and then remain latched as it moves ventrally in conjunction with the mandible during suction generation (Elad et al. 2014). In contrast, in the middle portion of genioglossus, the ventral electrode fired earlier than the dorsal electrode, which is likely driven by the pumping action of the tongue during suckling. It is likely that the ventral portion of the muscle is acting to stabilize the tongue, while fibers extending dorsally are likely concentric during contraction to depress the tongue. Finally, the most extreme variation we found along the dorsoventral axis occurred in the posterior region of the tongue. The dorsally placed electrode in some individuals only registered swallows, or registered swallows at a different time than sucks. In contrast, the ventral electrodes were active for every suck and showed little inter-individual variation. This further suggests that the ventral fibers of genioglossus may be acting to stabilize the tongue and resisting deformation of the floor of the mouth. The dorsal fibers, however, are likely assisting with movements of the tongue associated with propelling the bolus from the oropharynx into the esophagus, and likely are active concentrically as the motor of movement for the swallow. Future work synchronizing deformation of the tongue with regional heterogeneity in activity would test these possibilities. The regional heterogeneity along this axis further supports the need to consider the muscles of the tongue hydrostat based on neuro-motor region, rather than as anatomically discrete units (Liu et al. 2009; Wrench 2024).

Limitations

While these data are suggestive of nuanced regional divisions of function within muscles of the mammalian tongue, there are several limitations to this work. While we have data on regional heterogeneity in activity patterns across anatomical and spatial scales, our hypotheses on tongue function are dependent on validation from synchronous EMG and deformation data (which can be captured through paired radio-opaque beads fluoromicrometry, Camp et al. 2016). Future work should confirm these hypotheses, and also test how variable environmental or ontogenetic conditions, such as variation across nipple types during suckling, or variation through weaning, are related to variation in the functioning of the tongue musculature. Finally, much of the variation in our data lies in subtle differences in electrode positioning across individuals. Future work should attempt to map out discrete motor unit pools in conjunction with deformation and activity to attempt to delineate the regional heterogeneity in function more precisely.

The neural control of the tongue

Our data documents variation at multiple levels of hierarchy within a muscle. One level, variation among individuals, could arise from a combination of two factors. First, the muscles of the tongue have small motor units and the precision of our fine-wire electrodes allow us to record from a small number of muscle fibers (Mu and Sanders 2010). Thus, a few millimeters of difference in electrode placement within a named muscle could cause them to record from different motor units that fire at different times. However, even if the electrode was recording from the same motor units, different animals may cycle the use of their motor units differently over the course of a feeding session (Thexton et al. 1998). This has been observed as variation in EMG signal within a single electrode-pair in one animal over time (Holman et al. 2012; Konow et al. 2010).

A second potential explanation for inter-individual variation in activity within a muscle which has received insufficient attention is the presence of within muscle variation in EMG activity (but see Holman et al. 2012; Konow et al. 2010; Mayerl et al. 2022). As a muscular hydrostat, the tongue carries out multiple functions (sucking, transport, swallowing) during feeding. These functions also occur simultaneously in several behaviors, including during suckling. Within each of these functions, there are multiple biomechanical tasks required, which also occur at the same time and use the same structures. These tasks include forming a "shape" of the tongue, such as forming an effective seal around a nipple to generate suction, but the tongue must also position itself relative to other anatomical structures, including the hard palate, velum, and epiglottis (German and Crompton 1996; German et al. 1992). Thus, while genioglossus anatomically spans most of the length, depth, and width of the tongue, its fibers, driven by small motor unit innervation, function entirely differently in different regions, and play a role in both shape and positioning. While the intrinsic muscles of the tongue are anatomically distinct from the extrinsic muscles (Gray 1918; Kayalioglu et al. 2007; Wealing et al. 2019), contracting small groups of fibers in different regions, or co-contracting these fibers with neighboring or complementary fibers from the extrinsic muscles can produce widely varying movements. Thus, the general distinction between extrinsic muscles moving the tongue, and intrinsic muscles shaping the tongue, is an oversimplification at best, and at worst contains little biological value or meaning and misguides investigations of tongue form-function relationships (Schwenk 2001a; Schwenk 2001b; Wrench 2024).

Heterogeneity in activity and function stems from the distinctive anatomy of the tongue. Most of the muscles have only a single bony/cartilaginous attachment, with many insertions into other muscle fibers or the epithelium/connective tissue of the surface of the tongue. Yet many muscles, including the genioglossus, run the length of the tongue and span a large region. The interactions amongst the muscles, let alone within a muscle, can be complex, with the same muscle contracting eccentrically, isometrically, or concentrically depending on the activity of the other muscles. Variation in activation patterns within these muscles make the complex behavior of sucking possible by enabling the muscles to perform multiple tasks at once (e.g., stabilization of the anterior tongue around the nipple vs. depression/elevation cycles in the mid-tongue) (Johnson et al. 2023; Thexton et al. 1998). To understand the complex interactions of intrinsic and extrinsic tongue muscles, using named muscles as our unit of analysis is flawed. These muscles have multiple lines of action, vary between and across behaviors, with small motor units, and exhibit regional variation in activity patterns.

Conclusions

Together, these data suggest that the characterization of muscles in the tongue hydrostat as "extrinsic" or "intrinsic" does not accurately reflect either their neural control or their biological role (Schwenk 2001a; Schwenk 2001b; Wrench 2024). The "extrinsic" and "intrinsic" muscles likely play hybrid roles in both shaping and moving the hydrostat. Furthermore, the small motor units in the muscles of the tongue, the regional variation in control of those motor units, and the potential for one muscle to act through separate mechanisms depending on the behavior of interest and the region, suggest that there is a need to think about this hydrostat in terms of functional units, rather than anatomically defined structures (Liu et al. 2008; Liu et al. 2009; Mu and Sanders 2010; Schwenk 2001b; Steer et al. 2023; Wrench 2024). While the surface of the tongue is the proximal actuator for moving food and liquid from the oral cavity through the pharynx and to esophagus, understanding the biomechanical mechanism that causes that movement requires us to appreciate the motor control of the specific muscle fibers that create that surface. The use of anatomy as a predictor of function is thus unlikely to have a strong explanatory power, unlike in many muscles in the locomotor skeleton (Hermant et al. 2017; Ishikawa et al. 2025; Stavness et al. 2012). It is therefore critical for studies attempting to either model the function of this hydrostat, or to understand mechanisms underlying pathophysiologic functioning to do so in the context of neural control rather than arbitrary anatomical systems. Instead, the unit of function appears to be more regional, and a function of the specific task being performed.

Author contributions

Conceptualization: C.J.M.; Experimental Design: C.J.M., E.B.K.; Surgical procedures and animal care: C.J.M., E.B.K., M.E.K., H.E.S., A.E.S.; Data collection: C.J.M., E.B.K., M.E.K., H.E.S., A.E.S.; Data processing: C.J.M. and E.B.K. Manuscript Writing: C.J.M. Manuscript Editing: All authors.

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

We declare no competing interests.

Data availability

Data used in statistical analyses are available on Figshare at 10.6084/m9.figshare.28941305.

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