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COMPLEMENTARY SESSION PAPER

Evaluating the Impact of Nipple Design on Tongue Function in Infant Feeding Using a Dynamic Endocast

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Synopsis The mammalian tongue is a muscular hydrostat composed of multiple muscles, each with complex fiber architecture and small motor units. This allows it to move and deform in three dimensions (3D) to function in several complex behaviors, including suckling. The ability of infant mammals to successfully suckle is dependent on these variable deformations, as the tongue must perform multiple functions simultaneously. The lateral margins of the tongue curl to seal around a nipple, while the middle of the tongue moves in an anteroposterior wave to suck milk into the mouth, transport it posteriorly, and swallow it. The kinematics, mechanics, and coordination of the tongue during suckling are impacted by nipple properties, as evidenced by differences between feeding from nipples with narrow ducts (e.g., breastfeeding) and nipples that are hollow cisterns (e.g., bottle feeding). These structural differences result in different feeding outcomes, yet their effect on tongue function and kinematics is poorly understood. In addition, despite the 3D shape of the tongue during suckling, measurements of tongue movement have been limited to motion along the midsagittal plane and have not assessed suck volume. To evaluate how tongue function differs between ducted and cisternic nipples, we used X-ray Reconstruction of Moving Morphology and a dynamic endocast, synchronized with intraoral suction, to quantify 3D tongue kinematics and suck volume. We found that pigs generated less suction but had greater suck volumes when they fed on cisternic nipples compared to ducted nipples. This is likely because the pigs compressed the cisternic nipple to express milk, resulting in higher flow, which we hypothesize slowed the accumulation of suction and permitted the tongue to achieve a larger suck volume. These results suggest that nipple design impacts the relationship between fluid dynamics and tongue function during feeding. In addition, we found that infants moved the surface of their tongue ventrally and posteriorly throughout the suck, but they did not increase the width of the suck volume. The use of a digital endocast to measure suck volume represents an important advance in our ability to evaluate the mechanics of feeding and could be used in the future to understand the relationships between tongue function and performance as infants mature, as well as in a comparative framework.

Introduction

The mammalian tongue is a complex muscular hydrostat that functions across several behaviors, including respiration, vocalization, and most notably, feeding (Hiiemae and Crompton 1985; Hiiemae and Palmer 2003; Ludlow 2012; Jugé et al. 2023). As a muscular hydrostat, the tongue has no internal bones, and the muscles of the tongue act to both support and effect movement and shape change while maintaining a constant volume (Kier and Smith 1985). In addition, it can deform and move in complex three-dimensional ways, permitted by its complex muscle fiber architecture and having relatively small motor units (Mu and Sanders 1999; Kayalioglu et al. 2007; Wrench 2024). These characteristics are critical in the tongue's ability to change function across behaviors within a life stage, but also, to change in function across the lifespan.

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The importance of the ability of the tongue to adjust its function is perhaps most apparent when examining how it functions during feeding in infancy compared to adult feeding. In adults, food is acquired and processed via mastication with the teeth, and the tongue aids in this process by manipulating and positioning solid foods in the mouth prior to swallowing (Hiiemae and Palmer 2003; Feilich et al. 2021; Olson et al. 2021; Laurence-Chasen et al. 2023). However, during suckling, an essential behavior that infant mammals must perform to reach adulthood, the tongue is the primary structure used throughout the entire process (German et al. 1992; Thexton et al. 1998, 2004; Steer et al. 2023). An infant's tongue must curl around the nipple to form a seal, function as a pump to suck milk into the oral cavity, and then move in an anteroposterior traveling wave to maintain suction and transport milk posteriorly to be swallowed (Ardran et al. 1958; German et al. 1992).

Feeding in infants is thus a dynamic process that requires the tongue to function as a complex three-dimensional structure. This complexity can be compounded by changes in the sensory experience of an infant, and tongue function during infancy is known to vary based on both milk and nipple properties. For example, the way that the tongue functions to acquire milk changes at higher viscosity (Mayerl et al. 2021), and similarly, swallow function, powered by the tongue, is altered when viscosity is higher (Inamoto et al. 2013; Omari et al. 2013). Changes in nipple flow rate and nipple stiffness can also affect the rate of milk consumption, alter movements of the tongue, and alter the coordination of the tongue with other structures (Johnson et al. 2023; Steer et al. 2023). A common situation that requires the tongue to adjust its functioning, especially in humans, lies in differences in nipple design, particularly in regard to bottle feeding and breastfeeding.

Nipple design affects tongue function and feeding performance because it determines what mechanisms an infant can use to acquire milk during suckling. For example, a nipple that transmits milk in narrow ducts (as characteristic of most mammals) requires an infant to generate suction to draw milk into the mouth. In contrast, a nipple that is hollow (as seen in the teats of cows and goats [Weiss et al. 2004; Vesterinen et al. 2015; Adam et al. 2018]) permits an infant to compress the nipple to express milk and rely less on generating suction. Human breast tissue and bottle nipples lie on either end of this spectrum, and as a result infants use their tongues differently during breastfeeding and bottlefeeding. These differences in tongue mechanics are correlated with several differences in both feeding physiology and in health outcomes. For example, infants fed on breasts typically show decreased jaw motions and increased muscle activity during feeding (Inoue et al. 1995; Aizawa et al. 2010), and these biomechanical differences are correlated with breastfed human infants having decreased rates of malocclusion (Kobayashi et al. 2010; Romero et al. 2011; Chen et al. 2015; Peres et al. 2015; Thomaz et al. 2018), improved speech outcomes (Dee et al. 2007; Barbosa et al. 2009; Mahurin-Smith and Ambrose 2013; Mahurin-Smith 2015; Novayelinda et al. 2019; Moges et al. 2024), and decreased risk of cardiovascular disease (Li et al. 2024), all of which persist for several years after infancy. However, we have a limited understanding of the fundamental relationships between tongue kinematics, milk flow, and suction generation and how these relationships are impacted by nipple type, due to both methodological constraints and challenges associated with measuring infant feeding function.

One way to readily compare the effects of a ducted nipple design to a hollow, cisternic one is to create bottle nipples that differ only in their internal structure (Fig. 1) (Mayerl et al. 2024) (Kaczmarek et al. in review). When infants feed from a nipple that mimics the ducted anatomy of breast tissue, they generate more suction and compress the nipple less than when feeding from a cisternic nipple because the ducted nipple does not express milk when compressed (Mayerl et al. 2024) (Kaczmarek et al. in review). Nipple design thus impacts the relationship between milk flow and suction generation, both of which are driven by how the tongue is used to acquire and transport milk. To truly understand how these performance outcomes arise, we need to evaluate tongue function when feeding on both cisternic and ducted nipples.

Current methods for measuring tongue kinematics during suckling only quantify movement along the midsagittal plane. Ultrasound imaging along the midline of the oral cavity has been used to measure tongue motion relative to the hard palate in human infants (e.g., Geddes et al. 2018). These studies provide valuable insights into how the tongue functions during feeding, but they are often limited in that they evaluate only two timepoints in a given suck and in the number of sucks evaluated. In studies of non-human animals, radio-opaque markers are implanted in a series along the midline of the tongue, and their positions are tracked in X-ray videos (Gould et al. 2020; Mayerl et al. 2020, 2021; Johnson et al. 2023). These methods capture movement of anterior, middle, and posterior regions of the tongue, but only along the midline, and only at certain points along the midline. We do not know how the lateral regions of the tongue move during suckling (but

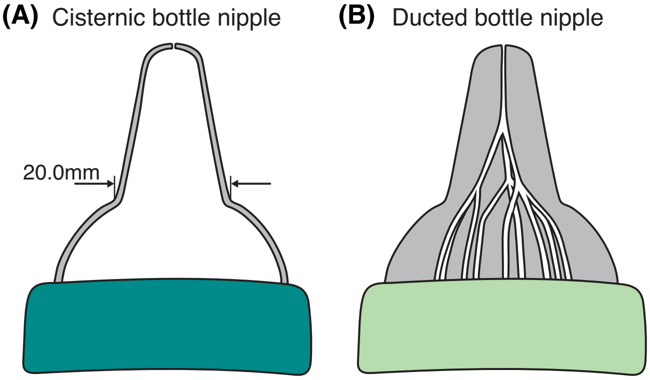

Fig. 1 Illustrations of the internal structure of the cisternic bottle nipple (A) and ducted bottle nipple (B). Both nipple types had the same size and shape, and the diameter of the nipples at the inflection point was 20.0 mm.

see Steer et al. 2023). In addition, tracking the motion of individual points in the tongue fails to account for how their movement contributes to suck volume three-dimensionally.

The dynamic endocast method for measuring volume change (Camp et al. 2015; Kaczmarek et al. 2025) can be used to address these methodological gaps and quantify suck volume (i.e., the portion of the intraoral space where suction is being generated to acquire milk). The dynamic endocast method was developed and validated for measuring intraoral volume during suction feeding in fishes (Camp et al. 2015, 2018, 2020; Gartner et al. 2022; Li et al. 2022; Whitlow et al. 2022; Kaczmarek et al. 2025). Dynamic endocasts are created from a constellation of virtual landmarks that are placed on, and move with, bone meshes and/or implanted markers that are animated using the X-ray Reconstruction of Moving Morphology (XROMM) workflow (Brainerd et al. 2010). A similar approach can be applied to measure suck volume and tongue kinematics during suckling.

In this study, our objectives were to (1) evaluate how the tongue moves during suckling, both along the midsagittal plane and mediolaterally, (2) quantify suck volume and its relationship to suction generation and tongue kinematics, and (3) test how nipple design affects tongue function and feeding mechanics. We studied suckling in infant pigs (*Sus scrofa*), a validated animal model for human infant feeding (German et al. 2017). We recorded high-speed X-ray video synchronized with intraoral pressure generation while infants fed on both ducted and cisternic bottle nipples, and then we reconstructed the suck volume using dynamic endocasts created from XROMM animations. We predicted that, in comparison to feeding on a cisternic nipple, infants would generate more suction with decreased maximum suck volumes when feeding on a ducted nipple, due to the constraints of needing to generate suction to acquire milk.

Methods

Animal housing and care

We obtained four infant pigs (Yorkshire/Landrace) at 24 h of age (Premier BioSource, CA, USA) and housed them in the Northern Arizona University vivarium. They were trained to feed on infant milk replacer (Birthright Milk, Ralco Show, Marshall, MN, USA) and raised on custom ducted bottle nipples. Animal care and experimental procedures were approved by the Northern Arizona University IACUC protocol #22-010 (Mayerl et al. 2019).

Nipples

Throughout their infancy, pigs were fed from a ducted bottle nipple that is designed to mimic mammalian breast tissue (see Kaczmarek et al., in review) (Fig. 1). To evaluate the impact of nipple design on feeding mechanics, we also fed infants from a hollow, cisternic nipple during data collection (detailed below). The general nipple design protocol follows methods described by Kaczmarek et al. (in review). Briefly, both nipple types were cast in silicone using 3D-printed molds. The ducted nipple is silicone (Ecoflex 00-10; Smooth-On, Inc., Macungie, PA, USA) with multiple branched ducts passing through it, and the cisternic nipple is hollow with walls of silicone (Dragon Skin 20A; Smooth-On, Inc., Macungie, PA, USA). The silicone materials used to create the ducted and cisternic nipples were selected to ensure that both nipple types had similar stiffness (i.e., force required to compress the nipple by 50%; see Kaczmarek et al., in review for details). We also ensured that the flow rates of the two nipples were similar through calculations using Poiseulle's law and by validating passive flow rates experimentally.

Marker implantation

We anesthetized infant pigs using isoflurane (2%–4%) and surgically implanted radio-opaque tantalum markers (beads) in multiple oropharyngeal structures at 4 and 14 days of age. We used custom-cut plunger rods and 18-gauge hypodermic needles to inject 0.8 mm beads and 21-gauge hypodermic needles to inject 0.5 mm beads. We injected ten 0.5 mm beads and nine 0.8 mm beads in the tongue (Fig. 2), five 0.8 mm beads in the submucosa of the hard palate, and one 0.5 mm bead into the skull (subdermally, in the dorsal surface of the snout). The beads in the tongue were arranged in five columns along the midline, lateral edges, and in between those columns (Fig. 2). We implanted an additional three 0.5 mm beads in the tips of both nipple types in a triangle pattern.

Data collection

Infants were raised feeding on the ducted nipple for 23 days (equivalent to approximately 9–11 months of human development, Eiby et al. 2013). At 23 days old, we recorded biplanar video fluoroscopy (OEC-9400, General Electric, Boston, MA, USA) with 12MP Redwood video cameras (IO Industries, Ontario, Canada) at 100 fps as the pigs fed on milk formula mixed with barium (E-Z Paque Barium Sulfate, EZ EM Inc., NY) to make the milk radio-opaque. Standard grids and a calibration object were used to remove distortion of the X-ray images and to calibrate the three-dimensional space (Brainerd et al. 2010). We inserted a pressure transducer through the nipple (3.5F Mikro-Tip Catheter Transducer; Millar Inc., Pearland, TX, USA), extending 1 cm beyond the tip of the nipple to collect intraoral pressure data, which we synchronized with the X-ray video using a 16 channel PowerLab (16–35, ADInstruments, Colorado Springs, CO, USA) at 10 kHz. All pigs were fed on both nipple types during the recording session. There was minimal variation in body position during feeding, and they stood without restraint with similar head postures. We recorded approximately 20 swallows per condition per pig.

We took a computed tomography (CT) scan of each pig post-mortem, using an Aquilion 64 CT scanner (Toshiba, Tokyo, Japan) with 0.235 mm × 0.235 mm pixel spacing and 0.5 mm slice thickness for three of the pigs (TD01, TD05, and TD09), and a SkyScan 1273 microCT scanner (Bruker, Billerica, MA, USA) with 0.052 mm pixel spacing and slice thickness for one pig (TD11).

Data processing

Skull kinematics and bead positions were reconstructed in three-dimensions using marker-based XROMM (Brainerd et al. 2010). Mesh models of the skull and the tantalum markers were segmented from the CT scans using 3D Slicer version 5.6.1 (Kikinis et al. 2014). The CT coordinates of the skull and hard palate beads were obtained in Maya (2024) using XROMM MayaTools scripts (developed by David Baier and Stephen M. Gatsey, available at https://bitbucket.org/xromm/xromm_mayatools/). All implanted markers were tracked in both X-ray videos using XMALab 2.1.0 (Knörlein et al. 2016; software and instructions available at https://bitbucket.org/xromm/xmalab). Unfiltered *xyz* coordinates of the markers and rigid body transformations of the skull were then exported from XMALab.

For each individual, we created one Maya scene (a "reference scene") that contained its skull polygonal mesh, an anatomical coordinate system (ACS) that we aligned and parented to the skull, and a plane that we aligned and parented to the midsagittal plane of the skull. The ACS was oriented such that the *x*-axis was anteroposterior, *y*-axis was dorsoventral, and *z*-axis was mediolateral. For each trial, we created Maya scenes that referenced the reference scenes, that contained the tracked *xyz* coordinates of the markers, and in which the skull mesh was animated by applying its rigid body transformation.

We tracked the position where the tongue sealed against the hard palate in Maya. The place where the tongue contacted the hard palate was apparent in the mediolateral X-ray video because the barium added to the milk made it much darker than the tongue and the hard palate. To track the position of the seal, we first created virtual X-ray cameras and video image planes in Maya (using XROMM MayaTools scripts). Then, we moved a locator to the position of the seal (when viewed using the mediolateral X-ray camera), keyed (i.e., locked) its position in numerous frames, and allowed Maya to interpolate between these positions. The mediolateral position of the locator was always on the midsagittal plane that was aligned to the skull. We will refer to this locator as the "tongue seal locator."

We used the position of the tongue seal locator to identify the timing of sucks. A suck started on the frame when the tongue seal initially formed and therefore was located the furthest anterior. A suck ended on the frame when the seal had moved furthest posteriorly, before the seal was released, and a new seal was formed anteriorly. We identified a total of 289 sucks across all four individuals ($N = 148$ when feeding from a cister-

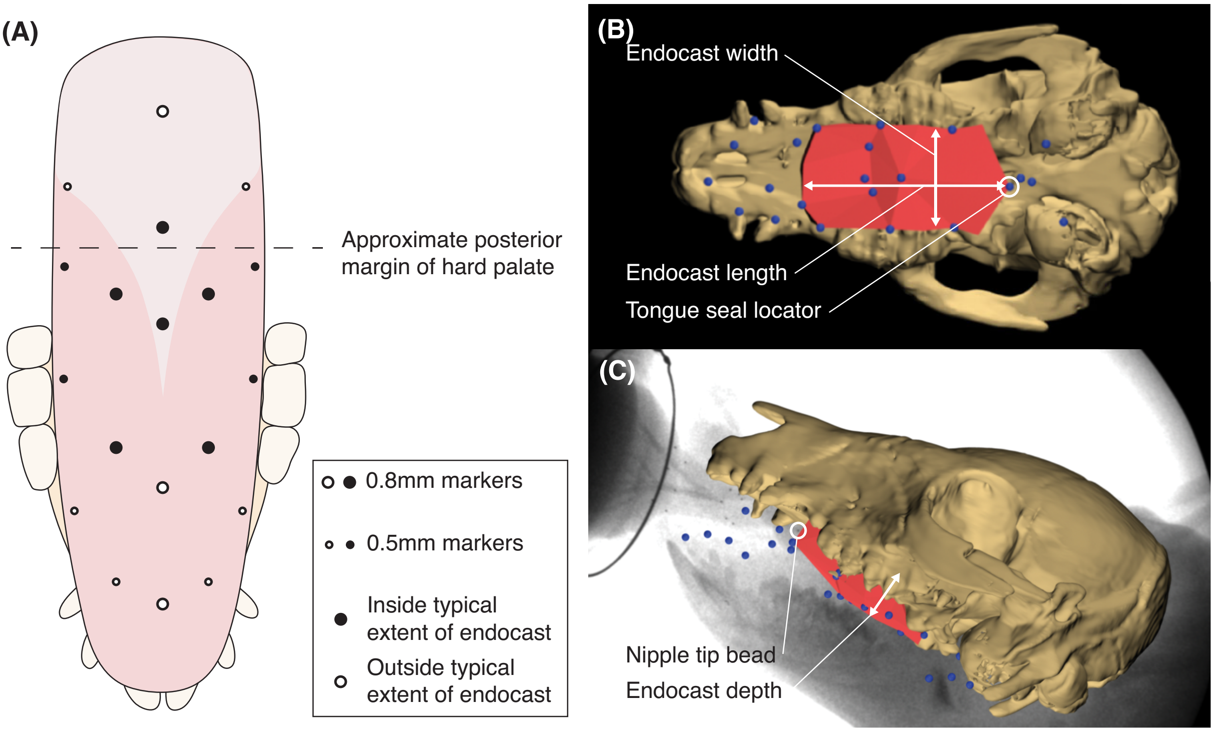

Fig. 2 (A) Illustration of the dorsal surface of the tongue showing generalized bead placement. Larger circles represent 0.8 mm beads, and smaller circles represent 0.5 mm beads. Filled in circles represent beads that were typically within the boundaries of the endocast (i.e., between the nipple tip and the position where the tongue sealed against the hard palate), while hollow circles represent beads that were often excluded because they were outside the boundaries of the endocast. The dashed line indicates the approximate posterior edge of the hard palate. (B) Ventral and (C) lateral views of a pig skull mesh model aligned to the X-ray video of an XROMM animation. Dark dots are animated beads implanted in the tongue, and the polygonal mesh in the mouth is the endocast of the suck volume.

nic nipple and $N = 141$ when feeding from a ducted nipple).

We processed the pressure data on a per suck basis. We converted the pressure data from mV to mmHg by multiplying by 41.3, a conversion factor that was determined empirically. Infants generate a small baseline amount of suction during suckling, i.e., subambient pressure that is maintained between sucks. We removed the contribution of this baseline suction by zeroing the pressure values for each suck to their maximum value (i.e., to the least amount of suction generation). In order to average pressure data across sucks, we converted time to a percentage of suck duration and downsampled the pressure data to 101 data points per suck using the spline method of the function approxm() from the package "FreqProf" (Epstein et al. 2016) in R (v4.3.1; R Core Team 2023, Vienna, Austria). We used these zeroed, splined, downsampled data to calculate the peak intraoral suction per suck.

Dynamic endocast

To measure the volume of the intraoral space where suction was generated during suckling, we created a dynamic endocast (Camp et al. 2015; Kaczmarek et al. 2025). Following previously established methods, the ventral, lateral, and dorsal boundaries of the endocasts moved dynamically with the movement of beads or locators that maintained fixed positions relative to the skull or the tongue. Specifically, the endocasts were bounded ventrally and laterally by the markers that were implanted close to the dorsal surface of the tongue and animated in Maya. The endocasts were bounded dorsally by 40–50 locators placed on the hard palate in a grid-like pattern in the Maya reference scenes.

However, unlike previous and validated applications of the dynamic endocast method (Camp et al. 2015; Kaczmarek et al. 2025), the anterior and posterior boundaries of the endocasts were not fixed relative to anatomical structures. These boundaries shifted so that the endocasts only captured the region of the oral cavity where suction was being generated. The endocasts were bounded anteriorly by the tip of the nipple and were bounded posteriorly by the tongue seal locator that we tracked in Maya. It was necessary for the boundaries to shift with the position of the tongue seal locator because tongue function is highly regional during suckling: in the beginning of each suck, the anterior region of the tongue is generating suction, but the posterior region of the tongue (posterior to the seal against the hard palate) is depressed in order to transport and swallow milk acquired during the prior suck. Therefore, the dynamic endocast encompassed a subset of the palatoglossal space because it only captured the space where suction was being generated to acquire milk. We will often refer to the endocast volume as the "suck volume."

To create the endocast, we exported the *xyz* positions of the beads and locators from Maya. In each frame, any beads or locators that were not between the anteroposterior positions of the tongue seal and the nipple tip were disregarded. Then, we used custom-written scripts (available at https://bitbucket.org/ArielCamp/dynamicendocast) that use the "alphashape" function in MATLAB (R2024a; MathWorks, Natick, MA, USA) to generate 3D shapes that enclosed the bead and locators in each frame and to calculate the volumes of these shapes. Alpha shapes are polygons constructed from a set of points using a specified alpha value to determine the fineness of fit to the points, and these polygons can include both convex and concave curvatures (Edelsbrunner and Mücke 1994). We used an alpha value of 1.5 because this created shapes that had the best and most consistent fit to the locators and beads, which we checked visually in Maya and by plotting volume over time for each trial.

To calculate the width, depth, and length of the endocasts, we made measurements directly from the positions of the beads and locators that were used to generate the endocasts. We used the XROMM MayaTools script "oRel" to calculate the position of the beads and locators relative to the skull ACS. Then, we used custom R scripts to calculate endocast width (defined as the maximum z-axis [mediolateral] distance between lateral bead locators), endocast height (defined as the maximum y-axis [dorsoventral] distance between the ACS and the midline tongue beads, i.e., tongue depression), and endocast length (defined as the x-axis [anteroposterior] distance between the nipple tip and the tongue seal locator), for each frame. To average these measurements across sucks, we converted time to a percentage of suck duration, and we used the approxm() function of the R package "FreqProf" to spline and upsample the endocast dimensions data so that each suck had 101 data points.

For each individual, we normalized the measurements of endocast volume, width, depth, and length to the maximum value (of each measurement) observed in that individual across all trials from both nipple types. This removed the effects of inter-individual variation in body size and bead placement. To quantify the effect of nipple type, we measured endocast volume, width, depth, and length at 12.5% of suck duration (referred to as the "beginning of the suck"), the time of maximum suction, and 85.5% of suck duration (referred to as the "end of the suck").

Statistical analyses

All statistical analyses were performed in R (v4.3.1; R Core Team 2023). We used linear mixed effects models and ANOVAs to evaluate differences in variables of interest (endocast volume, endocast width, endocast depth, and endocast length) by nipple type (i.e., ducted or cisternic), time in the suck (i.e., 12.5% of suck duration, time of maximum suction generation, and 85.5% of suck duration), and their interaction (Bates et al. 2015). In the linear mixed effects models, we modeled nipple type, time in the suck, and their interaction as fixed effects and individual as a random effect. If effects or their interactions were significant, we ran planned contrasts to calculate P-values for the effects and calculated Cohen's d to estimate effect size (Cohen 1992). We also evaluated differences in maximum pressure generation by nipple type by performing a two-sided two-sample unequal variances t-test.

Results

Dynamic changes in suck characteristics over time

When infant pigs fed from both cisternic and ducted nipples, we saw significant changes in endocast volume, depth, and length over the course of each suck, with all three variables increasing with time (Table 1, Fig. 3, Fig. 4). In contrast, the width of the oral cavity did not increase with time (Fig. 3, beginning vs. middle $t = 5.1$, $P < .001$, $d = 0.40$; middle vs. end $t = -5.3$, $P < 0.001$, $d = -0.52$, beginning vs. end $t = -0.28$, $P = 0.78$, $d = -0.02$).

The impact of nipple design on suckling

We found an impact of nipple design on several aspects of suckling mechanics. Maximum pressure generation per suck was smaller when pigs fed on a cisternic nipple than on a ducted nipple ($t = 6.8$, $P < 0.001$, $d = 0.8$, Fig. 4). In contrast, endocast volume was consistently larger when pigs fed on a cisternic nipple rather than a ducted nipple (Fig. 4, Table 1). This difference in volume between nipple types corresponded to differences in both the magnitude of tongue depression (i.e., endocast depth) and how far posteriorly the infants moved the seal between the tongue and hard palate (i.e., endocast length). Infants feeding on a cisternic nipple had a longer maximum seal length (i.e., endocast length at the end of the suck) than when feeding on a ducted

Table 1 Results of planned contrast and Cohen's *d* test comparing different time points in a suck within and between nipple types (*t*-statistic, *P*-value; Cohen's *d*).

	Cisternic: Beginning vs. Maximum Suction	**Cisternic: Maximum Suction vs. End**	**Ducted: Beginning vs. Maximum Suction**	**Ducted: Maximum Suction vs. End**	**Beginning: Cisternic vs. Ducted**	**Maximum Suction: Cisternic vs. Ducted**	**End: Cisternic vs. Ducted**
Comparison	**Time**	**Time**	**Time**	**Time**	**Nipple type**	**Nipple type**	**Nipple type**
Depth	**−18.6, <0.0001; −2.5**	**−13.7, <0.0001; −2.0**	**−12.1, <0.0001; −1.2**	**−8.3, <0.0001; −1.0**	*−4.8, <0.0001; −0.52*	1.7, 0.1; 0.20	**6.8, <0.0001; 0.96**
Length	**−22.1, <0.0001; −2.6**	**−26.9, <0.0001; −4.1**	**−19.7, <0.0001; −1.9**	**−23.8, <0.0001; −2.4**	*4.7, <0.0001; 0.53*	*6.5, <0.0001; 0.66*	**9.0, <0.0001; 1.4**
Volume	**−25.7, <0.0001; −3.0**	**−27.0, <0.0001; −4.1**	**−20.7, <0.0001; −2.1**	**−22.0, <0.0001; −2.2**	**7.0, <0.0001; 0.84**	**11.4, <0.0001; 1.2**	**15.8, <0.0001; 2.3**

Bolded values indicate a large effect size; italicized values indicate a medium effect size. "Beginning," "maximum suction," and "end" refer to values measured at 12.5% of suck duration, the time of maximum suction, and 85.5% of suck duration, respectively.

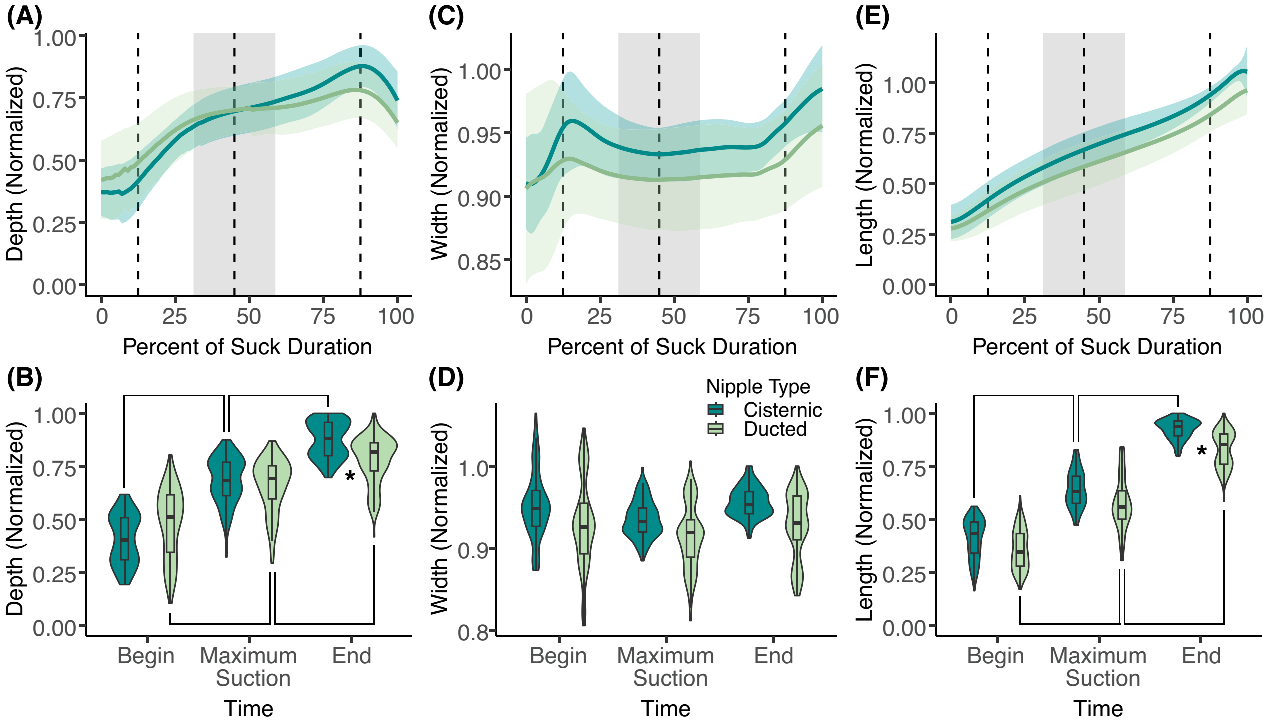

Fig. 3 Endocast depth, width, and length throughout the suck ([A], [C], and [E], respectively) and at specific time points ([B], [D], and [F], respectively) on cisternic (dark, $N = 148$ sucks) and ducted (light, $N = 141$ sucks) nipples. Endocast depth, width, and length were each normalized to the maximum value observed in each individual. The dashed lines in (A), (C), and (E) indicate 12.5% of suck duration, the average time of maximum suction generation, and 85.5% of suck duration, which correspond to the three time points compared in (B), (D), and (F): "begin," "maximum suction," and "end." The shaded regions in (A), (C), and (E) show one standard deviation in the timing of maximum suction generation. A solid line between time points and an asterisk between nipple types indicate a statistically significant difference with a large effect size.

nipple ($t = 9.0$, $P < 0.001$, $d = 1.4$), with medium effect sizes at the beginning and middle of the suck (Table 1, Fig. 3). Similarly, the largest difference in endocast depth occurred at the end of the suck, with pigs feeding on a cisternic nipple exhibiting greater tongue depression than when feeding on a ducted nipple ($t = 6.8$, $P < 0.009$, $d = 0.96$). In contrast, at the time of maximum suction, there was no difference in the endocast depth between nipple types, and at the beginning of the suck endocast depth was smaller when infants fed on

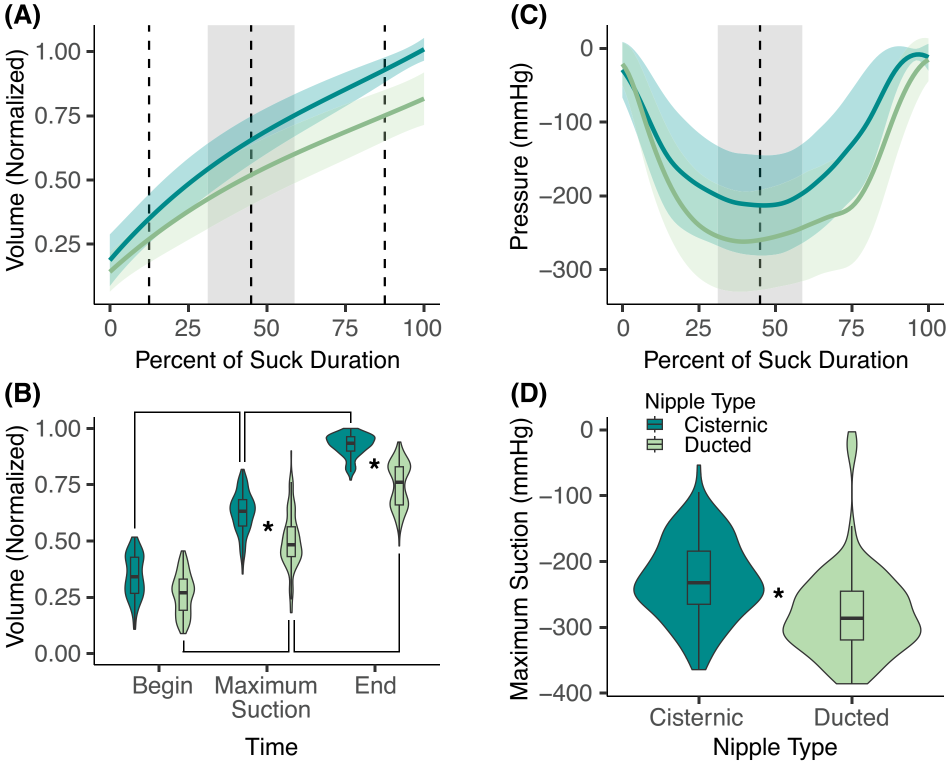

Fig. 4 Volume (normalized to the maximum value of each individual) throughout the suck (A) and at specific time points (B) on a cisternic (dark) or ducted (light) nipple. (C) Suction generation over the course of the suck and (D) the maximum suction on both nipple types. The dashed lines in (A) indicate 12.5% of suck duration, the average time of maximum suction generation, and 85.5% of suck duration, which correspond to the three time points compared in (B): "begin," "maximum suction," and "end." The dashed line in (C) represents the average time of maximum suction generation, and the shaded regions in (A) and (C) show one standard deviation in the timing of maximum suction generation. A solid line between time points and an asterisk between nipple types indicate a statistically significant difference with a large effect size.

the cisternic nipple than the ducted nipple, although with a medium effect (Table 1, Fig. 3). We did not observe a large effect of nipple type on the width of the suck volume, although we did see a medium effect size ($t = 9.02$, $P < 0.0001$; $d = 0.61$, Fig. 3).

Discussion

To acquire milk while suckling, infants must generate suction. This negative pressure is generated by using the tongue to first create seals around the nipple and against the hard palate and then increasing the volume of the intervening space. Here, we used a dynamic endocast to measure how infants increased their suck volume throughout each suck and test whether this varied based on nipple design. Infants changed both the depth (dorsoventral) and length (anteroposterior), but not width (mediolateral), of the intraoral space to create suction on both nipple types. Additionally, we found that the suck volume, length, and depth were higher at the end of the suck when infants suckled from a cisternic compared to a ducted nipple. Our data demonstrate that suckling is driven by changes in intraoral depth and length, and it is impacted by nipple design.

Changes in oral volume over the course of a suck

Previous research has developed a generalized model for the mechanics of mammalian infant suckling (Ardran et al. 1958; German et al. 1992; Geddes et al. 2008; Elad et al. 2014). The lateral margins of the tongue must curl around the nipple to create a seal, while concurrently the medial region of the tongue uses an anteroposterior wave-like motion to create negative pressure in the oral cavity to draw milk into the mouth (Thexton et al. 2004; Geddes et al. 2008; Elad et al. 2014; Steer et al. 2023). While this process has been visualized in two dimensions using ultrasound and X-ray imaging, kinematic data have been exclusively quantified from translation of the midline of the tongue (Thexton et al. 2004; Geddes et al. 2012; Johnson et al. 2023). These data treat suckling as a two-dimensional (2D) process and do not test the extent to which the tongue moves in three-dimensions (3D) during suckling. Creating dynamic endocasts of suck volume allowed us to quantify volume changes and kinematics in all three anatomical axes.

We found that during each suck, the endocast length (the distance between the tip of the nipple and the seal between the tongue and hard palate) and depth (the depression of the tongue) increased with time (Fig. 3). These data demonstrate that depression of the tongue works in combination with posterior movement of the tongue seal to increase oral volume and generate the pressure needed to acquire milk. This is consistent with foundational studies that showed that the tongue moves with an anteroposterior wave, translating the seal posteriorly as the suck progresses (Ardran et al. 1958; German et al. 1992; Thexton et al. 2004). The use of the endocast, in the context of variation in nipple design, provides novel insights into the limits of movement along these axes. The length of the intraoral space is likely dependent on how far into the mouth the infant positions the nipple and on the anteroposterior length of the hard and soft palates. Depth is likely constrained by the ability and space for the tongue to depress, so the floor of the mouth may dictate the maximum depth at which the tongue can be depressed.

Unlike depth and length, we found no changes in the endocast width throughout a suck. The width of the oral volume may not change because it is constrained by the width of the hard palate and upper teeth or by the thickness of the nipple and the requirement to form a seal around it. With these anatomical constraints in mind, it is understandable that we only observed modulation in the depth and length of the intraoral space. However, width might differ if infants were provided with bottle nipples of different diameters, and this could, in turn, affect suck volume, a possibility that we were unable to evaluate due to the two nipple types we evaluated having equivalent dimensions. The creation of the dynamic endocast for suckling supports previous work delving into mechanisms of feeding performance and also adds insights into potential constraints associated with suckling.

The impact of nipple design on infant feeding physiology

Although infants rely on suction generation to acquire milk during breastfeeding, infants feeding on bottles also acquire milk by compressing the nipple to express milk (Geddes et al. 2008; Aizawa et al. 2010; Sakalidis et al. 2012; Cannon et al. 2016). Our data parallels these differences between breastfeeding and bottle feeding, as we found that when feeding on a cisternic nipple, pigs generated less suction than when they fed on ducted nipples (Fig. 4). This suggests that they did not need to generate as much suction to acquire milk because they were compressing the nipple, as was quantified by Kaczmarek et al. (in review).

While one might expect that greater maximum suction generated on ducted nipples would correspond with greater suck volume, we found that infants had larger suck volumes when feeding on the cisternic nipple. The primary means by which infants achieved greater suck volume when feeding on a cisternic nipple were increasing the magnitude of tongue depression (i.e., endocast depth) and posterior movement of the seal (i.e., endocast length) by the end of a suck. Endocast length and depth were only significantly different between nipple types at the end of the suck, even though volume was greater across all time points.

This contrast, where infants generated less suction and achieved greater maximum suck volumes on cisternic nipples, is likely due to the use of both nipple compression (milk expression) and suction generation, thereby increasing milk flow during each suck. When flow is higher, we expect that less suction will be generated for the same amount and rate of intraoral expansion because milk flow will equalize the pressure differential more quickly. Similarly, if flow is higher and less suction is generated, the resistance to moving the tongue is likely also lower, and the tongue may move more easily than when suction generation is higher. This hypothesized relationship between milk flow, suction generation, and tongue movement likely explains why infants achieved larger endocast volume, depth, and length while generating less suction when feeding from the cisternic nipple relative to the ducted nipple.

This explanation is supported by qualitative differences in the rate at which pigs increased the depth of the intraoral space. When infants fed from the cisternic nipple, endocast depth increased at a fairly steady rate throughout the entire suck, consistent with our hypothesis that the tongue was able to move more easily with less resistance from large intraoral suction. In contrast, when infants fed on a ducted nipple, they appeared to quickly reach a maximum depth that was smaller than the maximum depth reached on the cisternic nipple. They reached their maximum depth near the time of peak suction, and they maintained this depth throughout the rest of the suck (while the tongue seal continued to move posteriorly to increase volume and maintain suction). This is consistent with our hypothesis that flow is slower on a ducted nipple (because expression cannot be used to supplement flow), that suction builds more quickly and to a higher peak, and that the tongue experiences resistance to movement during the period of maximum suction. Future analyses of the temporal relationship between the rate of tongue depression and intraoral suction may help reveal how tongue movement is both generating suction and constrained by it, depending on milk flow (e.g., differences in nipple compressibility, nipple flow rate, or the addition of thickeners to the milk).

Maximum endocast length was greater when infants fed from a cisternic nipple compared to a ducted nipple (Fig. 3). This difference may indicate that infants moved their tongue seal (i.e., contact between the tongue and the palate) further back on the hard palate when feeding on the cisternic nipple. Alternatively, it may indicate that the infants positioned the ducted nipple further into the mouth, which would reduce the maximum endocast length (i.e., distance between nipple tip and tongue seal), even without a difference in how far they moved the tongue seal relative to the hard palate. Prior research has shown that positioning a cisternic bottle nipple further into the mouth is correlated with weaker suction generation and less milk acquisition (Mayerl et al. 2020); however, we only observed smaller suck volumes on the ducted nipples, not reduced suction generation. This is likely due to differences in nipple design, as the change in how milk is acquired (suction vs. expression) may impact these relationships.

Ontogenetic and evolutionary implications

While these data represent an important step toward understanding the mechanics of suckling in 3D space, they are limited in that we analyzed data at only one time point during infancy and in only one species. It is well known that there are ontogenetic changes in suckling physiology and functional outcomes, the mechanics of suckling, and how tongue function during sucking is coordinated with swallowing and breathing (German and Crompton 1996; Gewolb and Vice 2006; Amaizu et al. 2008; Taki et al. 2010; Sakalidis et al. 2013; Bond et al. 2020; Mayerl et al. 2020, 2021). Infant anatomy also changes drastically through ontogeny, and a hallmark of mammalian development is postnatal elongation of the face (Zelditch et al. 1992; Helm and German 1996; Cardini and Polly 2013). This results in changes in the line of action of the muscles associated with feeding, including the tongue, and thus may impact physiologic functioning (Mayerl et al. 2021). The dynamic endocast can be used to test hypotheses about how ontogenetic changes in anatomy and physiology impact the functioning of the tongue as individuals mature and transition to feeding on solid foods.

In addition, although there is limited comparative data on suckling mechanics (Mayerl and German 2023), the little data that do exist demonstrate that species vary in their suckling mechanics. For example, some mammals with shorter oral cavities (e.g., felids and primates) exhibit a single seal between the tongue and the hard palate, whereas mammals with longer oral cavities (e.g., pigs and possums) tend to form seals in two places (Mayerl and German 2023). Exploring whether these changes occur through ontogeny as an individual's oral cavity lengthens would reveal whether differences in the contact between the tongue and palate are dependent on oral cavity length or are characteristic of a species because of their ancestry.

Furthermore, the mechanics of intraoral transport appear to differ across species (German et al. 1992). While most mammalian nipples contain narrow ducts, this anatomy varies from narrow passages to cisternic sinuses (Vesterinen et al. 2015; Adam et al. 2018; Mota-Rojas et al. 2024; Müller et al. 2024). As suggested by studies of cisternic and ducted bottle nipples (these data; Kaczmarek et al. in review; Mayerl et al. 2024), it seems likely that infants of species with cisternic teats (e.g., cows) express milk (by compressing the nipple) and generate less suction than infants of species with narrow ducts (most mammals). Similarly, there is varying neuromotor plasticity in the control of the tongue during suckling across mammals, suggesting further potential avenues of exploration (Gordon and Herring 2008). Creating dynamic endocasts of suck volume across multiple species would reveal variation in the mechanics of milk acquisition and transport and how these functional differences correlate to differences in morphology and physiology.

Clinical implications

Our data demonstrate that nipple type impacts tongue function (specifically, maximum tongue depression, suck volume, and suction generation), which likely corresponds to other metrics of feeding performance. The larger suck volumes acquired on cisternic nipples (Fig. 4) likely correlate to larger boluses, which in turn have been demonstrated to increase the risk of aspiration (Mayerl et al. 2021). Furthermore, Mayerl et al. (2024) found that, even while swallowing large boluses, infants raised on ducted bottle nipples had lower rates of aspiration compared to infants raised on cisternic bottle nipples. This suggests that aspiration risk is dependent on *how* boluses are acquired (i.e., how the tongue functions during suckling on different nipple types), in addition to *how much* is acquired. Further research is needed to understand how tongue movement and swallow characteristics relate to aspiration risk, and using dynamic endocasts to measure suck volume and dimensions could help reveal whether variation in tongue function is a fundamental driver of aspiration risk.

Methodological considerations and limitations

The dynamic endocast method was created to measure absolute volume and the rate of volume change of a 3D region during a behavior of interest in an XROMM animation (Camp et al. 2015; Kaczmarek et al. 2025). Accurate measurements of volume change rely on consistent but mobile anatomical boundaries of the endocast so that volume changes can be confidently attributed to expansion or compression of the specified region, not to inadvertent shifts in the boundary positions or changes in the how much tissue is included inside the endocast (Kaczmarek et al. 2025).

However, unlike previous applications of the dynamic endocast method (Camp et al. 2015, 2018, 2020; Gartner et al. 2022; Li et al. 2022; Whitlow et al. 2022), our endocasts were created with shifting boundaries based on the position of the nipple tip (anteriorly) and the position of the tongue seal against the hard palate (posteriorly). This was necessary because the tongue performs multiple functions synchronously—as a new seal is forming anteriorly between the tongue and hard palate, the posterior region of the tongue is continuing to move posteroventrally to transport and swallow milk from the previous suck. We isolated the region anterior to the seal with the hard palate where suction was being generated.

While this compromised our ability to analyze the absolute volume or rate of volume change of our endocast, that was not a goal of our analysis. Rather, we were interested in the effect of nipple type, which we were able to analyze because each individual fed on both nipple types, and endocast locators and markers were placed once per individual, making the endocasts comparable across each individual's trials.

Conclusions

We created dynamic endocasts with shifting anteroposterior boundaries to isolate the region of the intraoral space where suction was being generated. We found that endocast depth and length, but not width, increased throughout each suck, causing suck volume to increase and suction to be generated. There were significant differences in how this was accomplished across nipple types, where infants generated less suction and reached larger maximum suck volume, depth, and length when feeding on cisternic nipples compared to ducted nipples. We hypothesize that this initially surprising relationship results from infants compressing cisternic nipples more, causing milk flow rate to increase and subsequently reducing the build-up of suction as the tongue depresses. This suggests that movement of the tongue both generates suction and is constrained by it, depending on milk flow rate. These data represent the first quantification of suck volume during suckling and reveal that the relationship between suck volume and suction generation is dependent on nipple design and the capacity for nipple compression.

Further, by investigating suckling in 3D, we found that most of the variation occurs in 2D. While the tongue is a 3D structure, the increase in oral volume that generates suction may occur kinematically in 2D. Endocast width did not change throughout the suck and was not significantly different across nipple types. This suggests that, depending on the question being asked, quantifying suckling kinematics in two dimensions (dorsoventral and anteroposterior) may capture the primary ways that the tongue moves to generate suction without overlooking important biological variation. However, the lateral regions of the tongue still play an important role in suckling by maintaining a seal around the nipple. While kinematics and the dynamic endocast method may not quantify the quality of the seal around the nipple, future studies could measure force applied to the nipple to assess the function of the lateral regions of the tongue.

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Conflict of Interest

The authors declare no competing or financial interests.

Data availability

All data used in statistical analyses are available at www.doi.org/10.6084/m9.figshare.29602199.

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