Epaxial and hypaxial co-contraction: a mechanism for modulating strike pressure and accuracy during suction feeding in channel catfish

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Summary Statement

Channel catfish vary suction feeding performance by modulating co-contraction of epaxial and hypaxial muscles.

Abstract

Most fish species use concentric epaxial and hypaxial contractions to suction feed, whereby both muscle groups produce cranial expansion and negative intraoral pressures. In contrast, channel catfish (*Ictalurus punctatus*) suction feed with little to no cranial elevation and epaxial shortening, generating suction power primarily with hypaxial shortening and pectoral girdle retraction. We hypothesized that channel catfish 1) actively anchor the head via isometric contraction of the epaxials and 2) vary feeding performance by modulating the absolute and relative outputs of the co-contracting muscles. We used a combination of electromyography, intraoral pressure recordings, specimen manipulation, and developed a new dual-lever model to explore this idea. We detected epaxial and hypaxial co-contraction prior to suction force development in all strikes. Our model revealed that the differential between the co-contracting muscles may be used to modulate suction pressure and strike accuracy.

INTRODUCTION

Muscle contractions are often divided into isometric, concentric, and eccentric contractions. As any muscle may experience all three types of contraction during an activity, muscles can be more generally described as motors and anchors that generate and resist movement, respectively (Camp, 2019;

Camp et al., 2020). Motor-like muscle contractions are ubiquitous in vertebrates, as tetrapods and non-tetrapods alike use these contractions to generate positive mechanical work for movement. Vertebrates often rely upon a coupling of eccentric and concentric contractions whereby shortening of one muscle causes lengthening in another. Mammal limb muscles (flexors and extensors; (Cohen and Gans, 1975), bird flight muscles (depressors and elevators; (Dial et al., 1988), and fish swimming muscles (left and right axial muscles; (Jimenez and Brainerd, 2021; Schwalbe et al., 2019) provide just a few examples of muscles displaying paired eccentric-concentric contractions. Although eccentric and concentric couplings are ubiquitous, it is less common to identify coupled isometric and concentric contractions. Here we hypothesize that channel catfish (*Ictalurus punctatus*) use an isometric-concentric coupling to provide an important combination of stability and power production for suction feeding.

In most fishes, the epaxial and hypaxial muscles both function as motors during suction feeding—actively shortening to expand the buccal cavity, creating negative intraoral pressures that suck prey into the mouth (Camp and Brainerd, 2022). Although the cranial musculoskeletal system is highly interconnected (Camp and Brainerd, 2015; Olsen et al., 2017), each half of the axial musculature actuates a different part of the head. Epaxial muscles elevate the neurocranium and power dorsal expansion (Camp et al., 2015), whereas hypaxial muscles retract the pectoral girdle and power ventral expansion (Camp et al., 2020, 2018; Van Wassenbergh et al., 2005). In many fishes, epaxial and hypaxial muscles synergistically contract along two-thirds of the body to produce powerful suction strikes (Camp and Brainerd, 2022; Camp et al., 2015; Jimenez and Brainerd, 2020). Concentric contraction of these muscles can be reasonably inferred from the motion of bones to which they attach. Epaxial shortening can elevate the neurocranium anywhere between 5 and 50 degrees (Camp, 2021; Jimenez et al., 2018; Lauder and Liem, 1981). Hypaxial shortening can retract the pectoral girdle 1 to 18 degrees in a range of freshwater and saltwater fishes (Camp and Brainerd, 2014; Li et al., 2022; Lomax et al., 2020).

A recent study showed that channel catfish (*Ictalurus punctatus*) generate substantial pectoral girdle retraction with little to no neurocranial elevation (Camp et al., 2020), suggesting that some fishes use parts of the trunk muscles for active isometric stabilization. This prior study, which did not include electromyography (EMG) to measure muscle activity, hypothesized that channel catfish use paired concentric and isometric contractions to suction feed, where isometric epaxial contractions forcefully anchor the head, while concentric hypaxial muscle contractions generate most of the suction power by retracting the pectoral girdle (Camp et al., 2020). Here, we used EMG to test whether the epaxials are actively anchoring the head, with the alternative being passive stabilization. We also hypothesized that catfish modulate co-contraction of the epaxial and hypaxial muscles either to increase suction pressure by firmly stabilizing the neurocranium or to increase accuracy by allowing downward head movements that position the mouth toward prey. To test this hypothesis, we developed a dual-lever model that combines

electromyography and morphometric data to measure how mechanical interactions between the epaxial and hypaxial muscles impact suction feeding pressure.

MATERIALS AND METHODS

Animals and Training Protocol

Channel catfish (*Ictalurus punctatus*) were purchased from Osage Catfisheries in Osage Beach, Missouri, USA. Fish (standard length, SL 28.3 cm, 29.4 cm, and 30.1 cm for Cat1, Cat2, and Cat3, respectively) were housed at Brown University in tanks at room temperature. During their acclimation period, catfish were fed carnivore pellets. Two weeks prior to surgery and experimentation, we decreased feeding frequency to increase their appetite. During feeding experiments, food was placed at the bottom of the tank. Food items consisted of a combination of bisected night crawlers (*Lumbricus terrestris*), algae wafers, and carnivore pellets to elicit a range of strike intensities. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Brown University and followed guidelines and policies set forth by the IACUC.

Electrode Construction and Implantation

Bipolar electrodes were built from 0.1 mm diameter, Teflon-insulated, stainless-steel wire. Two 4-foot-long wires were twisted together, with an added tighter twist on the last 2 cm of the implanted end, where the tips of the recording end were 3 mm and 5 mm. From the offset recording end of the electrode, approximately 1 mm of insulation was removed from the tip of the wire. Additionally, approximately 3 mm of insulation was removed from the non-recording end of the electrode. Connector pins were soldered onto the non-recording end of the electrode after the insulation removal. The recording end of the electrode was bent to create a hook and was placed inside the beveled opening of a 21-gauge needle, with the rest of the electrode wire and leads with attached connector pins hanging from the outside of the needle. Electrodes were positioned to measure EMG in both the epaxial and hypaxial muscles. A total of four electrodes were placed in alignment with the anterior point of the dorsal fin, sampling the dorsal and ventral regions of the epaxials and hypaxials (Fig. 1A). Data from all four electrodes were used in our model, but only the dorsalmost and ventralmost electrodes were used for timing data. Electrodes were placed in six other positions but will be examined in a future analysis.

Surgical Procedures

Two separate surgeries were performed on each fish: a cranial cannulation surgery and an electrode implantation surgery. Both surgeries used the same anesthetic procedure. Fish were anesthetized via immersion in 0.12 g/L sodium bicarbonate-buffered MS-222 (Tricaine methanesulfonate) for 15 to 30

minutes. Fish were then placed in a surgical tray with a flow of oxygenated 0.10 g/L MS-222 and intubated to deliver oxygen and anesthesia to the gills. Water from the tray was dripped on the fish to prevent drying of the skin and eyes during surgery. The surgery for cranial cannulation was performed first, at least 10 days prior to experimentation and electrode implantation day. Using a micro drill bit set, a hole was drilled in the skull of the fish 1 cm from the tip of the rostrum, and a 6-inch-long cannula (Intramedic PE-90, outer diameter 1.27 mm) was inserted into this hole and held from falling out by heat shrink tubing (Fig. 1A). The electrode implantation surgery was performed on the day of experimentation, during which the intraoral pressure transducer was also placed inside the cannula. For each electrode, we used a 21-gauge needle to insert the electrodes at an angle to the surface of the skin, placing the recording tips within the white musculature at the midpoint between the skin and the vertebral column. Each individual was instrumented with 10 electrodes: eight on the left side, two on the right side. To relieve tension on the wires from fish movements, we sutured wires onto the body at multiple sites. Wires from the left and right side were then glued together (E600 flexible craft adhesive) to form a common cable. Finally, the length of the cable was surrounded with a series of polyethylene tubes, each 1 to 2 inches long, to float the cable and prevent tangling.

Data Collection and Processing

Electromyographic and pressure signals were recorded at a sampling rate of 4000 Hz. EMGs were amplified by 1,000 or 10,000, depending on signal strength (A-M Systems Differential AC Amplifier: Model 1700). Low-pass and high-pass hardware filters were set to 10 kHz and 100 Hz, respectively. A 60 Hz hardware notch filter was also used to reduce noise from ambient AC circuits. PowerLab data acquisition hardware (model 16/35) and LabChart software were used for analog-to-digital conversion and recording of EMG and pressure signals (AD Instruments, Sydney, NSW, Australia). EMG signals were rectified and software-filtered using the biosignalEMG package for R-studio (https://CRAN.R-project.org/package=biosignalEMG). Rectified data were processed with a Butterworth filter with low-pass and high-pass settings of 1 kHz and 100 Hz, respectively. Finally, we calculated a 5 ms moving average to create an envelope of the rectified-and-filtered signal to calculate normalized activation intensity for muscle force estimates (Jimenez and Brainerd, 2020; Jimenez and Brainerd, 2021). Buccal pressures were measured with a Millar SPR-407 pressure transducer, which was also plugged into the PowerLab. Pressure data were smoothed in R Studio using the smooth.spline() function.

Specimen Manipulation

We prepared a dead catfish specimen for physical manipulation. We removed skin and muscle from the body, taking care to avoid damaging any cartilaginous or bony structures which may serve to impede mechanical movement. We next restricted lateral movements of the specimen by placing a plastic grid (egg crate panels) on both sides of the body. The panels were restrained by threading two wires through the grid (one just caudal to the operculum and one medially located on the catfish), and securing the wire to the grid to limit lateral movement and dorsoventral flexion caudal to the operculum. Next, a hole was drilled using a micro drill bit approximately 5 mm caudal to the tip of the nose and a wire was inserted into the hole. With the specimen restrained laterally, a digital scale was used to determine the amount of force necessary to produce dorsiflexion in the anteriormost intervertebral joints.

Dual-lever Model

To understand axial mechanics, we developed a dual-lever model to predict intraoral pressure output for each strike (Fig. 1 C-D). The epaxial system is modeled as a first class lever that produces neurocranial elevation (developed by Carroll et al., 2004) and the hypaxial system is modeled as a third class lever system that retracts the pectoral girdle and depresses the lower jaw complex. The model output was the pressure exerted in buccal cavity by each out-lever. In the dorsal lever, the epaxial muscle applies a force to the neurocranium (in-lever) that gets transmitted to the dorsal surface of the mouth (out-lever). Our prior work has shown that the axis of rotation for the neurocranium in some fishes is caudal to the cranivertebral joint and ventral to the post-temporal supracleithral joint (Jimenez et al., 2018), but given the lack of actual neurocranial rotation in channel catfish, we used the craniovertebral joint as the fulcrum. In the ventral lever, the hypaxial muscle applies a pressure to the pectoral girdle (in-lever) that gets transmitted to the ventral surface of the mouth (out-lever). We calculated input and output pressures using morphological measurements, published physiological data, and our EMG data (Fig. 1). We measured lever arms, cross-sectional areas, and projected areas of the mouth from one individual as all fish were of similar size. For each region surrounding an electrode, we calculated muscle force capacity by taking the product of isometric stress, cross-sectional area, and normalized activation intensity (Jimenez and Brainerd, 2020). The exact value used for the isometric stress of fish white muscle will shift the slopes of our regression models, so we choose the value 150 kNm^{-2} or 150 kPa, based on hypaxial tetanic stress in another catfish species but of a similar size to those in our study, approximately 7 cm in cranial length (Van Wassenbergh et al., 2007). Normalized activation intensity for each electrode was calculated by dividing all voltages by the highest voltage, typically observed in a fast start (swimming data will be analyzed in a future study). This provides an estimate of the percentage of muscle fibers active within each muscle region for each suction strike, allowing us to make strike-specific estimates of

muscle force and pressure. Thus, rather than calculating the theoretical maximum pressure that could be produced by an individual fish or species, our model allows us to examine the musculoskeletal mechanics of suction feeding in a wide range of biologically relevant performance levels, not just when pressure is maximized. Furthermore, we developed a metric called "mechanical synergy" that describes the relative strength of the dorsal and ventral pressure outputs in the mouth. We define mechanical synergy in terms of relative strength ($P_{strong}/P_{weak} \times 100$) for statistical analysis, where a value of 100% indicates the dorsal and ventral pressure outputs are identical.

The dual-lever system generates suction either by forcefully rotating both levers in opposite directions or by forcefully stabilizing one lever while the other is forcefully rotated. This characterizes the two main expansion strategies used by suction-feeding fishes: species which use dorsal and ventral muscles to generate power and species which generate suction power with only the ventral expansion system, like the channel catfish (Camp et al., 2020). An important assumption is that both of the out-levers interact with each other anatomically and hydrodynamically. Epaxial and hypaxial muscles generate opposing torques on the vertebral column during suction feeding. Epaxials dorsiflex the intervertebral joints. Hypaxials retract the cleithrum and, once the cleithral-supracleithral joint can no longer rotate, ventroflex the intervertebral joints. If only the hypaxial lever is actuated, with no opposing epaxial torque, the vertebral column may ventroflex either during cleithral retraction or after peak cleithral retraction. The epaxial and hypaxial levers are hydrodynamically connected since pressure in the mouth is uniformly distributed. Whether the mouth is open or closed, hypaxial contraction alone will function as a piston that produces negative buccal pressures that will ventroflex the neurocranium or vertebral column, as ventroflexion requires less force than dorsiflexion. Consequently, our model predicts that muscular energy intended for suction can be lost in the form of vertebral flexion when pressure outputs to the buccal cavity vary greatly.

Statistical Analysis

All data processing, filtering, and statistical analyses was performed in R Studio (RStudio Team, 2020) using native functions. When data normality was not met, data were either log or square-root transformed for linear regression. We used a p-value significance threshold of 0.05 for all statistical tests.

RESULTS AND DISCUSSION

Timing of Muscle Activation and Intraoral Forces

Muscle activity was detected in both the epaxial and hypaxial muscles in all 118 feeding strikes from three channel catfish (Fig. 2). The timing of muscle activity and intraoral pressure changes varied within and among individuals, but we observed important similarities. Onset times for hypaxial and

epaxial muscle were both statistically significantly earlier than the onset of pressure changes in each individual (p < 0.01, ANOVA followed by Tukey post-hoc tests; Fig. 2B). Epaxial and hypaxial activity preceded the onset of pressure changes by 11 ± 1 ms and 16 ± 1 ms, respectively (mean $\pm$ s.e. n = 118 for all pooled strike data). Time to peak pressure was 36 ± 3 ms, and the durations of epaxial and hypaxial activity were 47 ± 11 ms and 51 ± 16 ms, respectively. As the time to peak force production of white muscle fibers ranges from 10 to 20 ms, the relative timing of our data indicate that the epaxial and hypaxial muscles both generated force during suction feeding (Altringham and Johnston, 1990; Carroll et al., 2009; Van Wassenbergh et al., 2007). Peak subambient buccal pressures were -15 ± 1 kPa and ranged from -0.17 to -69 kPa. Peak pressures were highly variable within individuals and were significantly greater for Cat2 and Cat3 as compared to Cat1 (p < 0.01, ANOVA with Tukey post-hoc tests). The greatest recorded subambient pressures were similar to the greatest values recorded for similarly sized catfish (Camp et al., 2020), suggesting we elicited a biologically relevant range of performance levels.

Morphology and Specimen Manipulation

Channel catfish possess a nuchal plate comprised of robust supraneural bones that spans from the supraoccipital crest to the first dorsal fin spine (Rodiles-Hernández et al., 2010). Post-mortem manipulation of the axial skeleton in one individual revealed that morphology of the anterior vertebral column, which includes the nuchal plate and Weberian apparatus, substantially limits neurocranial elevation–or dorsiflexion of the vertebral column. Forces greater than 4.9 N were needed to produce any neurocranial elevation above the typical resting position, and even these large forces produced only a small amount of dorsiflexion. Gravity alone, or ~1 N assuming the head alone weighed 100 grams, was enough to depress the neurocranium. As species with densely packed axial skeletons tend to produce less neurocranial elevation (Jimenez et al., 2018), the robust axial morphology of channel catfish likely limits neurocranial elevation and, therefore, epaxial muscle shortening. In contrast, vertebral ventroflexion requires very little force and the pectoral girdle retracts freely in response to forces from the hypaxial muscles (Camp et al., 2020; Li et al., 2022).

Dual-Lever Model for Axial Muscle and Suction Mechanics

We found a statistically significant relationship between our predicted and measured pressure outputs for the epaxial and hypaxial lever systems (Fig. 3A). This result suggests that models with EMG intensity, muscle area, and lever arms as inputs can predict a range of suction feeding performance for both the epaxial and hypaxial lever systems. Regression statistics for the hypaxial and epaxial models were similar to each other, suggesting that an EMG-corrected lever model can reasonably predict per-strike suction pressures for both anatomical arrangements. Although R^2 values were low, the slope and y-

intercept fits were reasonable given the assumptions of our model. We also found that the mechanical synergy of the epaxial and hypaxial levers—measured as the similarity between their out-lever pressures—limits suction pressure (Fig 3B). These results support the hypothesis that in order to generate strong subambient suction pressures, the hypaxial and epaxial muscles must transmit both high and similar amounts of pressure to their out-levers. If the pressure outputs are equal but low, buccal pressures will be low. If the pressure outputs are vastly different, then energy that would otherwise produce suction will instead flex the body. Thus, without isometric epaxial contractions, catfish risk losing muscular energy in the form of ventroflexion of the vertebral column (Fig. 3C). However, vertebral flexion is not necessarily detrimental to the success of the feeding strike. Body bending may allow fish modulate its attack and better direct the mouth toward its prey, thereby increasing strike accuracy. This may be especially true for benthic feeders such as catfish, which feed in complex environments where directed strikes could be critical for prey capture. Therefore, epaxial contraction can be used to either rigidly stabilize the head in order to increase suction pressures or allow vertebral flexion to increase strike accuracy at the expense of suction pressures. This suggests a tradeoff exists between pressure and accuracy in the axial muscle of fishes, though detailed kinematic analysis and pressure measurements are needed to compare strike performance in forward and bottom feeding.

Our dual-lever model differs from the original lever model pioneered by Carroll et al. (2004) in two important ways. Rather than predicting the upper limits of suction performance for individual fish and species, our model estimates strike-specific suction pressures using a combination of morphometrics and normalized EMG intensity (Jimenez and Brainerd, 2020; Jimenez and Brainerd, 2021). Additionally, our model describes how suction performance can be impacted by myriad mechanical interactions between the epaxial and hypaxial systems. For example, catfish epaxials have a low morphological potential that would normally suggest that the epaxials transmit low forces to the buccal cavity relative to other species. Epaxial mass is 45% of total axial muscle mass in catfish versus 65% in bluegill sunfish (Camp et al., 2018; Camp et al., 2020) and epaxial mechanical advantage is 0.25 in catfish versus 0.35 in bluegill sunfish (Carroll et al., 2004). However, we speculate that epaxial function remains unaffected by their smaller size and lower mechanical advantage. First, the roof of the mouth has a relatively fixed surface area compared to the floor of the mouth where the surface area increases from expansion of the hyoid apparatus. A given amount of epaxial muscle force (input) will result in higher pressures on the roof of the mouth (output) due to its smaller surface area (ignoring the known anatomical coupling of neurocranial elevation and hyoid depression (Muller 1987). Second, the force-velocity properties of muscle predict high forces from the epaxial muscle due to near-zero shortening velocities (Altringham and Johnston, 1990; Coughlin and Akhtar, 2015).

Despite some of these advantages, our model oversimplifies the musculoskeletal anatomy, muscle dynamics, and kinematics of the feeding apparatus. Fish have highly kinetic skulls with dozens of cranial bones and muscles, forming linkage systems that produce complex 3D motions (Aerts, 1991; Olsen et al., 2020; Westneat, 1990). Our model also assumes isometry for both muscles, so while the isometric muscle data used for our calculations should match *in vivo* muscle stress for the epaxial muscle since they shorten slowly, it will likely overestimate hypaxial muscle stress since these muscles shorten relatively fast (~ 0.1 versus ~1 Ls^{-1}; Camp et al., 2020). Furthermore, we measured cross-sectional area (CSA) when physiological cross-sectional area (PCSA) would have been more appropriate for force estimates. Yet, the axial musculature has a complex 3D fiber architecture that has recently been shown to experience dorsoventral strain gradients during feeding–precluding the use of traditional measurements in this system (Gemballa and Vogel, 2002; Jimenez et al., 2021). Therefore, this model cannot be used to predict or describe complex skeletal motion or the non-steady dynamics of the muscle system (Coughlin and Carroll, 2006). We are hopeful that the dual-lever model can still be used to study the diversity of cranial expansion strategies and examine how muscles work synergistically to produce suction feeding at a range of performance levels.

Conclusion

We conclude that channel catfish stabilize the neurocranium and vertebral column using isometric epaxial contraction, as the muscle always activates (this study) and shortens less than 1% during suction feeding (Camp et al., 2020). Additionally, we conclude that catfish generate suction power using concentric hypaxial contraction because the muscle is always active and always shortens 4 to 8 %, resulting in pectoral girdle retraction of 6 to 11 degrees (Camp et al., 2020). This concentric-isometric muscle synergy allows catfish to expand the oral cavity without losing substantial energy in the form of neurocranial depression or axial ventroflexion (Fig. 3). Thus, the ancestral motor pattern for suction-feeding fishes, simultaneously active hypaxials and epaxials (Alfaro et al., 2001), can be functionally important even for species primarily reliant on hypaxial-powered suction (although it is noteworthy that the epaxials are often silent during biting in parrotfish, suggesting muscle function can also change for different feeding modes) (Alfaro and Westneat, 1999). Our results also suggest mechanical tradeoffs exist between forceful and accurate strikes, as complex feeding maneuvers might require muscular asymmetries to produce downward strikes such as those routinely used by benthic species like catfish. It is unclear how this might differ from the asymmetries that arise during side strikes, where fish simultaneously produce dorsiflexion and lateral flexion during feeding (Jimenez et al., 2021). Future studies are needed to investigate how feeding performance is impacted under different ecological conditions.

Data Availability

Video, EMG and sonomicrometry data are available from ZMAPortal (zmaportal.org), study 'Catfish swimming and suction feeding EMG', permanent ID ZMA29.

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Figures
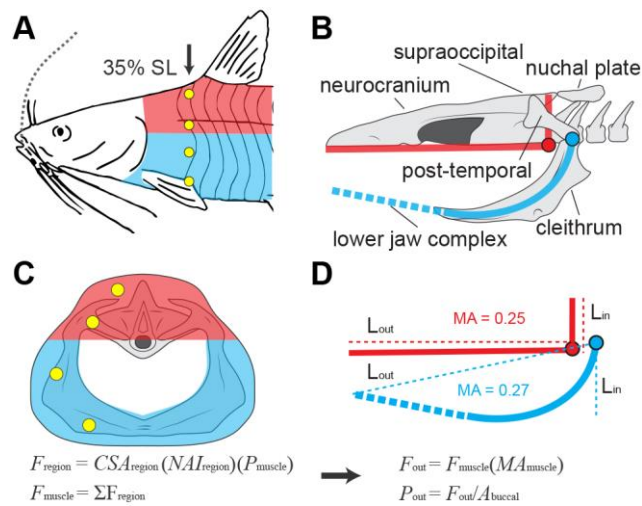
Fig. 1. Anatomy and dual-lever model parameters. (A) Instrumentation. Electrodes (yellow circles) implanted within the epaxial (red) and hypaxial (blue) muscles, and pressure transducer (dashed line) implanted through the neurocranium into the buccal cavity. (B) Dual-lever model. Epaxial muscle is modeled as a first-class lever with a fulcrum at the level of the vertebral column, an in lever on the posterior surface of the neurocranium, and an out lever on the roof of the mouth (Carroll and Wainwright, 2004). Hypaxial muscle is modeled as a curved third-class lever, with its fulcrum at the post-temporal supracleithral joint, an in-lever on the cleithrum, and an out-lever spanning the linear distance from the fulcrum to the anterior margin of the lower jaw complex (dashed blue line). (C) Cross-sectional view of musculoskeletal anatomy. Below: Equations for calculating regional muscle force (F_{region}) from cross-sectional area (CSA), normalized activation intensity (NAI; calculated as voltage divided by maximum voltage recorded in any swimming or feeding behavior per Jimenez and Brainerd, 2020) and published isometric muscle stress (P_{muscle}). Muscle force (F_{muscle}) is calculated as the sum of all F_{region}. (D) Moment arm lengths and mechanical advantage for the epaxial and hypaxial systems. Projected buccal areas of the roof and floor of the mouth (A_{buccal}; not shown) were also measured to calculate our model output, the epaxial and hypaxial pressures on each out-lever due to muscular contraction.
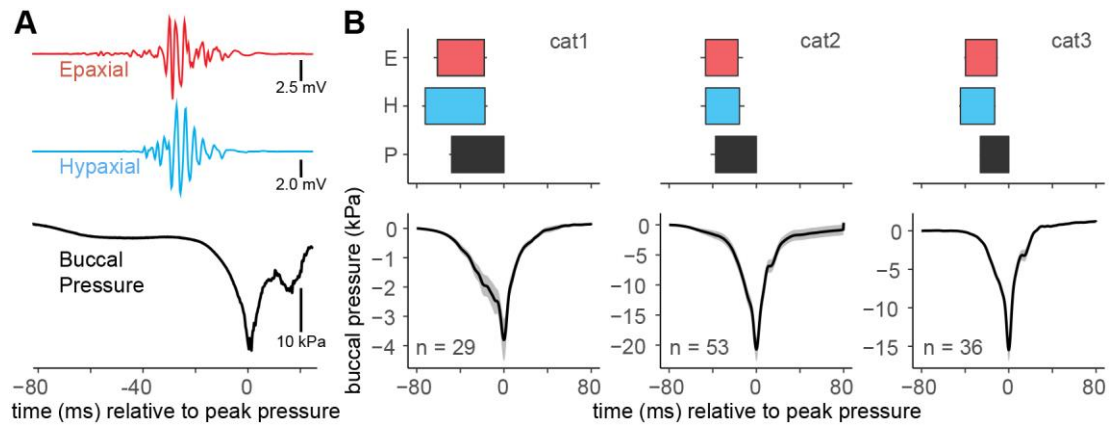
Fig. 2. Muscle activity precedes changes in buccal pressure. (A) EMG and pressure traces for a suction strike. (B) Mean muscle EMG onset and offset times along with buccal pressure for three catfish. In the bar graphs, the left and right edges of the bar are the mean onset and offset times, respectively. Error bars indicate standard errors. Length of the bar is the mean duration of EMG activity. Pressure traces show mean ± s.e.m at each time point. Only the dorsal epaxial and ventral hypaxial electrode data were used for this analysis. Number of strikes per individual are shown.
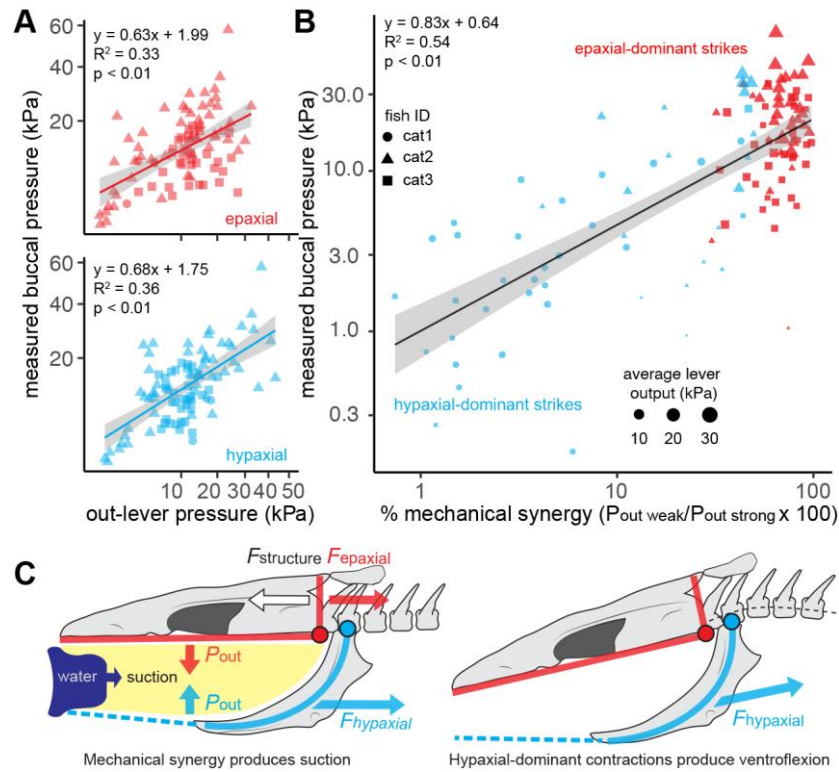
Fig. 3. Synergy of axial co-contraction can limit suction pressure on a per-strike basis (A) Buccal pressure (shown as absolute value of subambient pressure) is positively correlated with estimated out-lever pressures from both the epaxials and hypaxials. As trials with low muscle synergies produced low performance, we excluded any strikes with less than 10% mechanical synergy for this particular analysis. Exclusion of these trials produced a right skewed distribution, and the data were therefore square root transformed for regression analysis. (B) Buccal pressure is positively correlated with mechanical synergy, the similarity between out-lever pressures estimated for the epaxial and hypaxial muscles. Point size shows average lever output, which averages the per-strike out-lever pressures estimated for both muscle groups. As data were left skewed, both axes were log10 transformed for regression analysis. All strikes were included for this analysis. (C) Predicted skeletal motion with and without isometric epaxial activity. Mechanical synergy produces opposing forces that generate suction and prevent buccal pressures from depressing the neurocranium. Hypaxial contraction alone would ventroflex the vertebral column in addition to retracting the pectoral girdle. For examples of fish that use the epaxial lever for neurocranial elevation, see (Carroll et al., 2004)
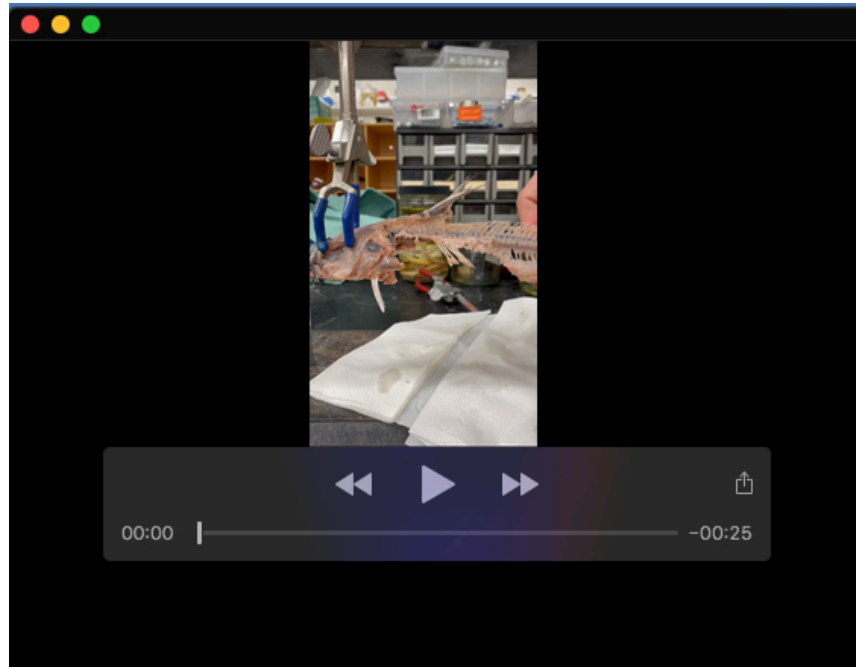
Movie 1. Physical manipulation of a dissected channel catfish. The vertebral column is bent ventrally and dorsally to show how axial morphology can limit neurocranial elevation.