RESEARCH ARTICLE

Regional Differences in Hyoid Muscle Activity and Length Dynamics During Mammalian Head Shaking

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ABSTRACT

The sternohyoid (SH) and geniohyoid (GH) are antagonist strap muscles that are active during a number of different behaviors, including sucking, intraoral transport, swallowing, breathing, and extension/flexion of the neck. Because these muscles have served different functions through the evolutionary history of vertebrates, it is quite likely they will have complex patterns of electrical activity and muscle fiber contraction. Different regions of the SH exhibit different contraction and activity patterns during a swallow. We examined the dynamics of the SH and GH muscles during an unrestrained, and vigorous head shaking behavior in an animal model of human head, neck, and hyolingual movement. A gentle touch to infant pig ears elicited a head shake of several revolutions. Using sonomicrometry and intramuscular EMG, we measured regional (within) muscle strain and activity in SH and GH. We found that EMG was consistent across three regions (anterior, belly, and posterior) of each muscle. Changes in muscle length, however, were more complex. In the SH, mid-belly length-change occurred out-of-phase with the anterior and posterior end regions, but with a zero lag timing; the anterior region shortened before the posterior. In the GH, the anterior region shortened before and out-of-phase with the mid-belly and posterior regions. Head shaking is a relatively simple reflex behavior, yet the underlying patterns of muscle length dynamics and EMG activity are not. The regional complexity in SH and GH, similar to regionalization of SH during swallowing, suggests that these anatomically simple hyoid strap muscles have more complex function than textbooks often suggest. *J. Exp. Zool. 315:111–120, 2011.* © 2010 Wiley-Liss, Inc.

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The supra- and infrahyoid musculatures are active during various mammalian head and neck movements (Thompson, '41; Brodie, '50; Doty and Bosma, '56; Forsberg et al., '85; Thexton et al., '98, 2007; Konow et al., 2010). Behaviors relying on this hyoid musculature include suckling, drinking, eating, vomiting, breathing, and extension/flexion of the neck (Forsberg et al., '85; van Lunteren et al., '87a,b; Thexton et al., '98; Lang et al., 2002). The evolutionary rationale for the form and function of the hyoid musculature in mammals is that the tasks of these muscles are not ones of strength, as is true of the muscles of mastication (Hiiemae and Crompton, '85). Their role is to move the hyoid precisely over short distances. As such, these muscles are referred to as classic parallel fibered strap muscles (Hildebrand and Goslow, 2001).

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Several muscles, in particular, sternohyoid (SH) and geniohyoid (GH), are antagonist strap muscles that are active during many of these movements and are important for moving and stabilizing the hyoid bone. Yet, little is known about fascicle strain heterogeneity in the hyolaryngeal musculature, and specifically whether the simple architecture of these muscles translates into homogeneous patterns of activity and length change.

Most studies of fascicle strain heterogeneity have examined vertebrate limb muscles. For example, the turkey lateral gastrocnemius shows superficial to deep regional fascicle strain heterogeneity during ramp lengthening (Roberts and Azizi, 2010), whereas the medial gastrocnemius in guinea fowl shows proximodistal fascicle strain heterogeneity during running (Higham and Biewener, 2008). Much of this work examines muscles that are biarticular and have pinnate fibers (Brainerd and Azizi, 2005; Azizi et al., 2008; Azizi and Roberts, 2009). Some nonpinnate muscles that have broad insertions, including the pigeon pectoralis, show complex fascicle strain heterogeneity (Soman et al., 2005). Here, heterogeneous fascicle strain over the cross-section of the muscle may be an anatomical avenue of streamlining the range of lengths across which the fascicles contract. There are other highly parallel-fibred limb muscles with heterogeneous fascicle strain along their proximodistal axis, such as the toad semimenbranosus (Ahn et al., 2003) and the human biceps brachii (Pappas et al., 2002).

There are few examples of data on muscle fascicle strain for oropharyngeal or hyolaryngeal muscles (van Lunteren et al., '87a,b, '89; van Lunteren and Dick, 2000; Konow et al., 2010). van Lunteren et al. suggest that the relationship between muscle length and function is complex during respiration, particularly in GH and SH. They found the GH to be lengthening while electrically active.

Recent work found that different regions of the SH have different contraction patterns. The anterior, mid-belly, and posterior regions exhibit different contraction and lengthening patterns during a swallow (Konow et al., 2010). When length change is measured for different regions within the same muscle, different regions (mid-belly vs. ends) change length at different times. Furthermore, when infant pigs swallow, muscle activity in the SH is most strongly correlated with shortening contraction of the mid-belly region. The mid-belly shortens more than the end regions, and this suggests that movements at the ends of the muscle are most likely influenced by antagonist muscles during swallowing (Konow et al., 2010). The patterns of EMG activity and strain in the SH and GH, however, have not been analyzed during other behaviors than swallowing.

Here, we examine the dynamics of the SH and GH muscles during a natural, unrestrained, and vigorous head shaking behavior in an animal model of head, neck, and hyolingual movement. Determining the muscle activity and length dynamics relationships during a cyclical, nonoral behavior that incorporates all the hyoid musculature permits us to compare EMG activity and determine relationships of length changes within and among muscles. Whether the same regionalization exists in this behavior as during feeding behaviors is not known. Therefore, we measured SH and GH regional activity and length dynamics, (i.e. length changes), to test the hypothesis that muscle activity and muscle length dynamics (lengthening/shortening) would be equivalent in all three regions during head shakes. Specifically, our hypothesis was that, given the regional differences seen in these muscles during feeding behaviors and respiration, there would be differences or asynchrony between regional activity and length change in the SH and GH during a vigorous head shake, so that interregional activity and length changes would occur asynchronously.

MATERIALS AND METHODS

Animals

The experiments were conducted at Johns Hopkins University and were approved under ACUC ♯SW07M14. The subjects were eight piglets from the Tom Morris Farm (Reisterstown, MD). Their body weights were 5–6 kg at an age of 10–16 days. Details about data collection were given in (Konow et al., 2010) and the methods are, therefore, reviewed briefly here.

Instrumentation of Muscles

The piglets were placed under anesthesia by 5% Isoflurane inhaled through a face mask. They were intubated, and aseptic conditions were maintained through the surgery. The sternohyoid, genioglossus, geniohyoid, and thyrohyoid were carefully exposed using blunt dissection (Sack, '82). Only one muscle, the SH or GH, was studied for length dynamics per animal. Figure 1 shows the EMG electrode and sonomicrometry crystal placements.

We did two sets of parallel studies: the first set of four experimental animals (C, D, M, S), focused on the SH and the second set (T, U, V, W) on the GH. For each set, the focal muscle was divided into three areas—anterior, middle, and posterior—by four 2 mm piezoelectric crystal (Sonometric Corp, London, ON). Between each pair of crystals, bipolar EMG patch electrodes were attached to the muscle surface. The crystals were evenly spaced, approximately 17 mm apart (Fig. 1). The crystals emit ultrasound energy across the distance they are placed. Therefore, changes in length can be recorded. For the first set of animals, bipolar patch EMG electrodes were attached to the surface of the SH muscle between each pair of crystals (Loeb and Gans, '86). In order to avoid any damaged muscle resulting from the crystal insertion, the electrodes were placed 3–4 mm away from the line of the crystals (Fig. 1).

We placed EMG electrodes in additional muscles that might be involved in the behaviors under study, or be antagonists to the SH or GH: the middle of the genioglossus, close to the origin of the TH, and the GH. EMG patch electrodes were placed on the surface of the GH, between the three crystal pairs. These four

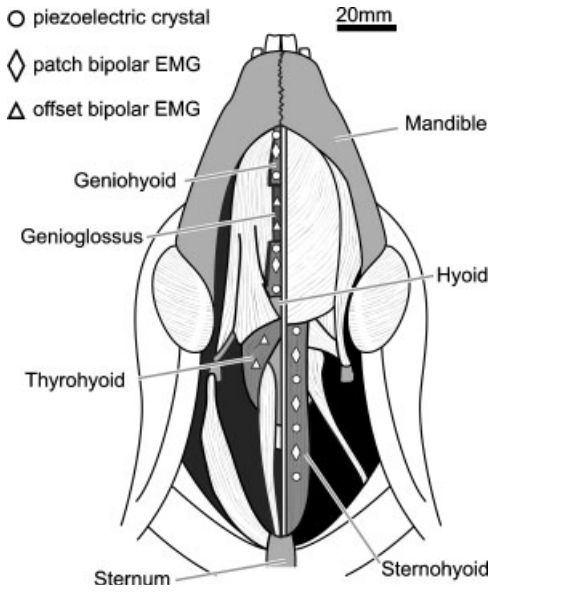

Figure 1. Ventral view of the supra- and infrahyoid muscles examined. Four 2 mm piezoelectric crystals were placed on the left aspect of the sternohyoid (SH), approximately 17 mm apart. The four crystals separated the SH into three regions: anterior, middle, and posterior. Bipolar EMG patch electrodes were attached to the surface of the SH between each pair of crystals. A similar instrumentation was used for the geniohyoid in the second set of animals.

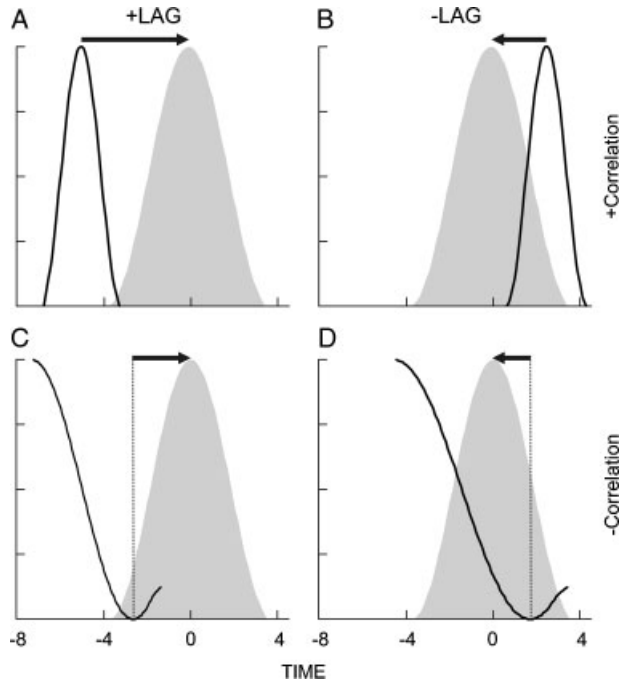

Figure 2. The principles of waveform cross-correlation analysis as used in this study. The cross-correlation function produces a lag, i.e. the relative timing cycles of two variables over time. If a wave from one variable lines up in time with a wave of a second variable, the lag = 0 and the activity is in synchrony. If there is a positive lag (**A**, **C**), the response vector (black line) must move in a positive direction to the target vector (grey shading). The opposite occurs in a negative lag (**B**, **D**); the response vector moves in a negative direction after to match the target vector. The *r*-value is the correlation between the two wave forms and measures the pair-wise correlation between two waves at a given lag. The lag with the highest *r*-value is the measure of the best fit of relative timing between the two waves. A negative *r*-value indicates an inverse correlation of a given lag; the *r*-value sign indicates whether the waves are in or out-of-phase with each other.

animals were additionally instrumented with fine wire bipolar electrodes in the TH and SH (Fig. 1). Before surgery, the sonomicrometry crystals had a skin button connector attached (Sonomicrometrics, London, ON) and the electrode wires had a microconnector attached (Glen-Air, Glendale, CA).

Recording Procedures

The wires from the crystals and electrodes exited out the ventral surface of the neck through a submandibular incision. The extra cutaneous wires were carefully folded and bandaged with Vetwrap (3M, MN), and the connectors were sutured to the bandage. The piglets recovered from surgery within 3–5 hr, and were fully alert and standing before feeding. Data was collected over a 36–48 hr period, during which the pigs were fed and data was recorded every 3–4 hr. We recorded length changes from the sonomicrometry crystals and EMG recordings from all the experimental muscles (Fig. 2) for swallowing, suckling, vocalization, and head shaking.

The piglet suckled from a baby bottle with a pig nipple (Nasco, Fort Atkinson, WI) while standing in a pet carrier. Several times during an experiment, we elicited a head shake by gently brushing inside one of the ears of the pig with a cotton swab. The pig reliably responded with vigorous side-to-side lateral head movement. After the experimental period, the pigs were placed in a deep plane of inhalant anesthesia and euthanized with veterinary euthanasia solution (IC). A postmortem dissection was conducted to verify electrode and crystal position.

A PC running Powerlab 16/30 recorded the data in LabChart v.6.1.3 (AD instruments, Colorado Springs, CO). The EMG signals were amplified 1,000 times with a MA-300 EMG system (Motion Lab Systems Inc, LA) and a high pass filter of 25 Hz was applied. The inputs to Powerlab, from the EMG amplifiers and sonomicrometer outputs, were digitized at 10 KHz. The sonomicrometer output was three crystal pair distances recorded at 508 Hz with a transmit pulse of 220 msec and inhibit delay set between 2.2–2.6 mm to condition the signals.

Head Shake Identification

Data sequences were selected with clear shakes, containing several revolutions of the head. The quality of a sequence was determined by the maximum number of channels recording data without artifacts or noise for all behaviors. From each data sequence, the head shakes were identified and found to be characterized by several short cycles of EMG activity across all six muscles and length changes in all the sonomicrometric channels.

The oscillations observed from the sonomicrometry crystal data consisted of two to eight revolutions (Fig. 2A) in both the SH and GH, and lasted approximately 300–800 msec with simultaneous isolated bursts of EMG activity for SH, GH, genioglossus, and TH. Each set of shake oscillations was copied into a separate data file and coded numerically. One hundred and fifty-two head shakes were compiled, 80 for the first four set of pigs, representing SH sonomicrometry data, and 72 for the second set of pigs, representing the GH sonomicrometry data.

Data Extraction

A script was coded in Matlab R2008a (v.7.6.0.3.2.4, The Mathworks, Natick, MA) to process the EMG signals (German et al., 2009). In brief, EMG signals were rectified and reset integrated to a period of 10 msec, with the baseline noise subtraction (Thexton et al., '98). Sonomicrometer signals were left unprocessed, other than a subsampling to 100 Hz to retain synchronization with the processed EMG signals.

In order to obtain a quantitative measurement and to evaluate synchronization, a cross-correlation analysis was run for each shake (Loeb et al., '87; Wren et al., 2006; Thexton et al., 2009). The cross-correlation function (CCF) output provides two pieces of information. First, it measures the time relationship or lag between two sets of time series data (Fig. 2). If a wave from one variable lines up in time with a wave of a second variable, then the lag = 0 and the activity is in synchrony. If there is a positive lag, the response vector must move in a positive direction (to the right) relative to the target vector in order to align (Fig. 2A).

The opposite occurs in a negative lag; the response vector moves in a negative direction (to the left) to obtain peak correlation with the target vector. The second item the CCF indicates is if the vectors are in-phase or out-of-phase. The *r*-value indicates the degree of correlation between the two wave forms; that is, the pair-wise correlation between two waves at a given lag. A negative *r*-value indicates an inverse correlation (out-of-phase waveforms) at a given lag (Fig. 2C, D).

Statistics

Cross-correlation analyses were done in SYSTAT 12 (2009). From this output, the lag with the strongest correlation was statistically determined. All identification of shakes in LabCharts, data extraction in Matlab, and assessment of shake quality were done by one person (SEW). We carried out several subanalyses on the CCF results (also in Systat 12) to test our hypotheses. First, we tested if the lags among crystal pairs were different from zero, using a repeated measures linear model, including individual as a factor. Then, we tested if the lags among EMG electrodes were different from zero, using repeated measures linear model, including individual as a factor. Lags with a negative correlation were tested separately from lags with a positive correlation. Multiple comparisons included Bonferoni corrections.

RESULTS

General Behavior

Animals responded reliably and consistently to a brushing with a cotton swab in their ear with vigorous head shaking. There was regularity in the revolutions, i.e. the individual movements of each shake, from midline to lateral, then contralateral and back to midline (Fig. 3A). In the shake shown in Figure 3, an upward line indicates lengthening of the muscle region. A downward line occurred when the muscle region was shortening. The bottom rows show the vigorous EMG activity during the head shaking behavior.

Sternohyoid

There were no differences in the timing of muscle length change between the anterior (hyoid) and middle region and between the middle and posterior (sternal) region (Table 1). The majority of the correlations for these two comparisons were negative, indicating an out-of-phase relationship (Figs. 4A, 5A, C). The average lag was zero, indicating that, on average, maximum shortening in one region occurred simultaneously with maximal lengthening in another. However, the wide spread of values and high variation in the timing lags between these pairs of regions suggests that either region could change length first, but that one was shortening while the other was lengthening. The relationship between anterior and posterior SH consistently returned a positive correlation, with an average lag of 4.02 msec (Figs. 4B, 5B). Again, there is large variation in the lag, including both positive and negative lag values. The mean lag of 4.02 msec suggests that length change in the anterior section tends to occur before the posterior (sternal) section.

The timing of differences in EMG activity between each pair of regions was not statistically significant (Fig. 6), i.e. the lag was not statistically different from 0.0 (Table 1). When comparing the EMG activity between the SH and other muscles, we found small but significant lags between both SH and TH and SH and GG. The lag between SH and GH was not statistically different from 0.0 (Table 1; Fig. 7A).

Geniohyoid

The timing of length change between the three pairs of regions in the GH included a large number of both positively and negatively correlated relationships (Table 2; Fig. 8). Despite a large variation in lag values, there was some clustering of values. Approximately

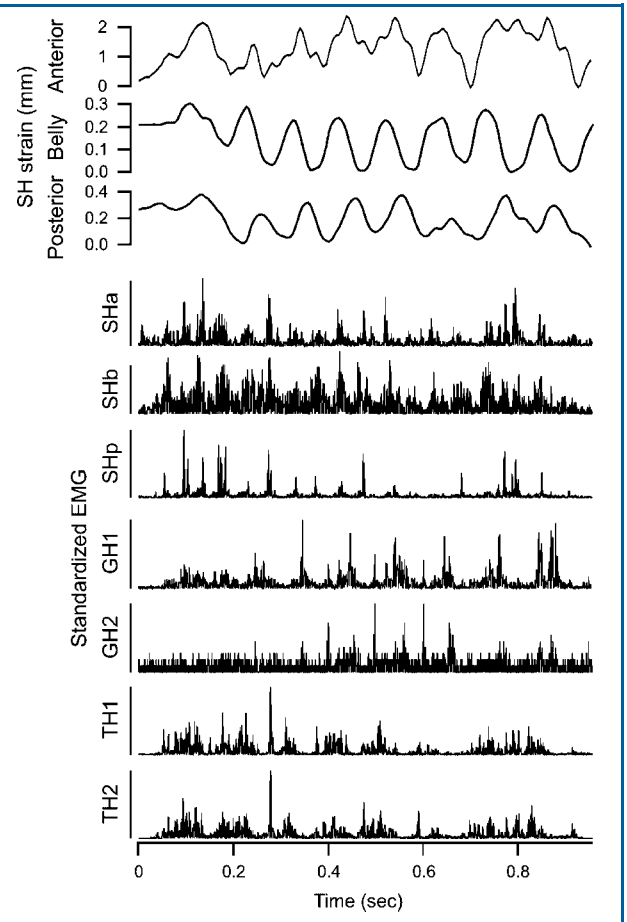

Figure 3. Raw time series data for shakes. Top three rows show sternohyoid (SH) sonomicrometry waves for the anterior (hyoid), belly, and posterior (sternal) regions. EMG is shown below for the same anterior (SHa) belly (SHb) and posterior (SHp) regions. Bottom four rows show duplicate EMG signals for the geniohyoid (GH) and the thyrohyoid (TH).

half of the anterior (mandibular) to middle distances had a negative relationship with no lag, but the other half had a positive relationship with a mean lag of −12.25 msec (Fig. 9A). The anterior to posterior (hyoid) relationship was generally positive, with a significant lag of 6.37 msec (Fig. 9B). The middle to posterior relationship was largely negative, but with zero lag, and high variation around that lag (Fig. 9C). The CCFs for the EMG activity between all region pairs returned positive correlations and lags that were not different from zero (Fig. 10). The CCF for EMG activity of GH relative to TH had a lag of 0.126 msec with positive correlation, whereas the EMG of GH and SH had no lag and positive correlation (Table 2; Fig. 7B).

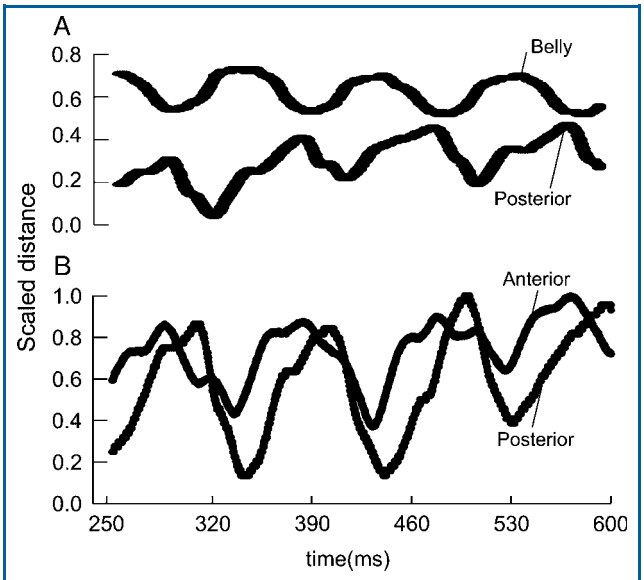

Figure 4. Regional strain heterogeneity in the sternohyoid. (A) The negative correlation of middle to posterior regions. (B) Positive correlation of anterior to posterior regions, at a slight lag. The anterior region lengthens slightly before the posterior region.

Table 1. Results of *t*-tests for SH group.

Regions tested	CCF correlation	df	Mean lag (msec)	SD (msec)	*t*-Value	*P*-value
aSH-mSH	Negative	50	0.19	10.23	0.13	0.894
mSH-pSH	Negative	64	−2.07	10.62	−1.57	0.122
aSH-pSH	Positive	60	4.02	11.2	2.79	0.007*
aSHemg-mSHemg	Positive	29	−1.94	8.71	−1.21	0.235
mSHemg-pSHemg	Positive	22	0.23	1.77	0.62	0.540
aSHemg-pSHemg	Positive	23	2.87	7.63	1.84	0.078
SHemg-THemg	Positive	54	−0.16	0.43	−2.78	<0.001**
SHemg-GHemg	Positive	42	0.01	0.19	0.23	0.82
SHemg-GGemg	Positive	64	−0.23	0.45	−4.05	<0.001**

*$P<0.05$; **$P<0.001$. H_o: mean lag = 0.

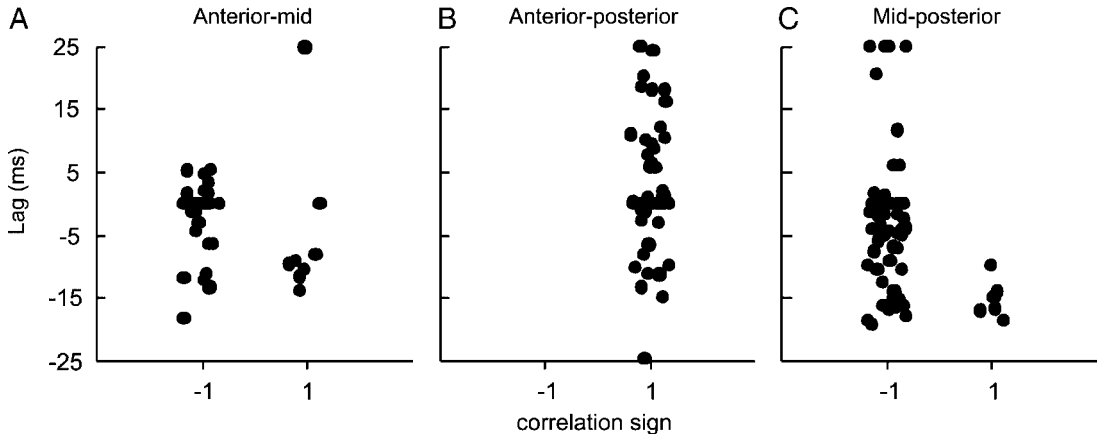

Figure 5. Results from analyses of sternohyoid regional strain. Each regional comparison produced a lag when negatively (−1) and positively correlated (+1). (**A**, **C**) The distribution of lags indicates that the origin insertion regions were negatively correlated (i.e. out-of-phase) and (**B**) from anterior to posterior, the regions are lengthening in-phase.

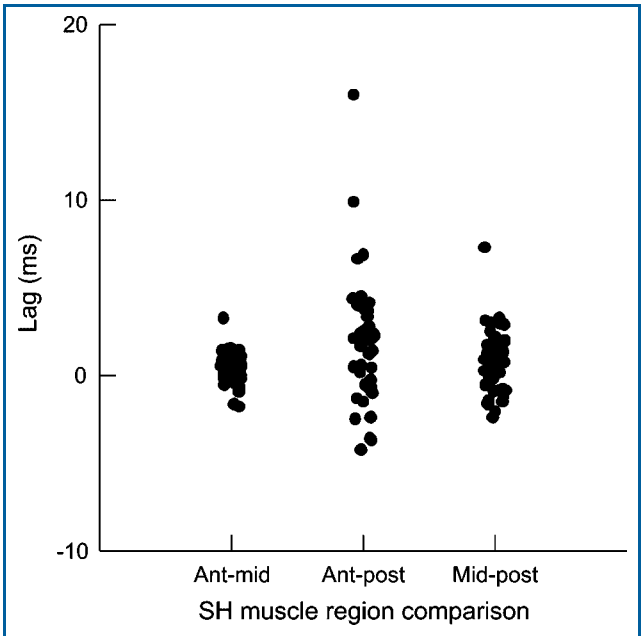

Figure 6. Results from analysis of sternohyoid (SH) regional EMG. Comparisons are: Ant-mid, anteriormiddle ($P = 0.235$); Ant-post, anterior–posterior ($P = 0.078$); Mid-post, middle-posterior ($P = 0.54$). $P > 0.05$ and, therefore, we accept Ho: mean lag = 0. The distribution shows points cluster at zero lag. SH shows homogeneity among regions in EMG activity signals.

DISCUSSION

Head Shake Muscle Activity

During a head shake, there were rhythmic bursts of activity across all hyoid muscles observed in this study. Contrary to our hypothesis, the EMG of the anterior, middle, and posterior regions in both the SH and GH was synchronous, with little variation in lag. The intermuscular comparisons of EMG highlighted more similarities than differences between hyoid musculature activities. The EMG of the SH and GH had zero lag and were, therefore, active at the same time; this is not surprising, given that the principal function of these antagonists would be to stabilize the hyoid bone during a vigorous behavior, such as a head shake.

There was a statistical difference in EMG between the SH and TH, as well as between the SH and genioglossus (Table 1). However, the activity lags between pairs of these muscles were in the range of 0.1–0.2 msec, for a revolution that lasted approximately 100 msec. The differences in activity timing of these muscles during a swallow is on the order of 20–50 msec, for a behavior that lasts about 400–500 msec (German et al., 2009). It is questionable whether the very small differences in EMG timing make a significant difference in the behavior. Likewise, the difference in timing between EMG of GH and TH is less than 0.15 msec (Table 2). Although statistically significant, the small magnitude of differences suggest that in terms of a single head shake revolution that lasts 100 msec, we are uncertain of their biological meaningfulness.

Head Shake Length Dynamics

The results from the comparisons of regional length changes were more complex than those for the EMGs. We found regional differences in strain heterogeneity in both SH and GH, as well as a high amount of variation in the timing lags among muscle regions. These regional differences are consistent with previous findings for the SH during swallowing (Konow et al., 2010). This supports our idea that the SH has complex behavior, even though its architecture is simple (Paniello et al., 2001; Peker et al., 2006). The most consistent results were that the ends of the SH were

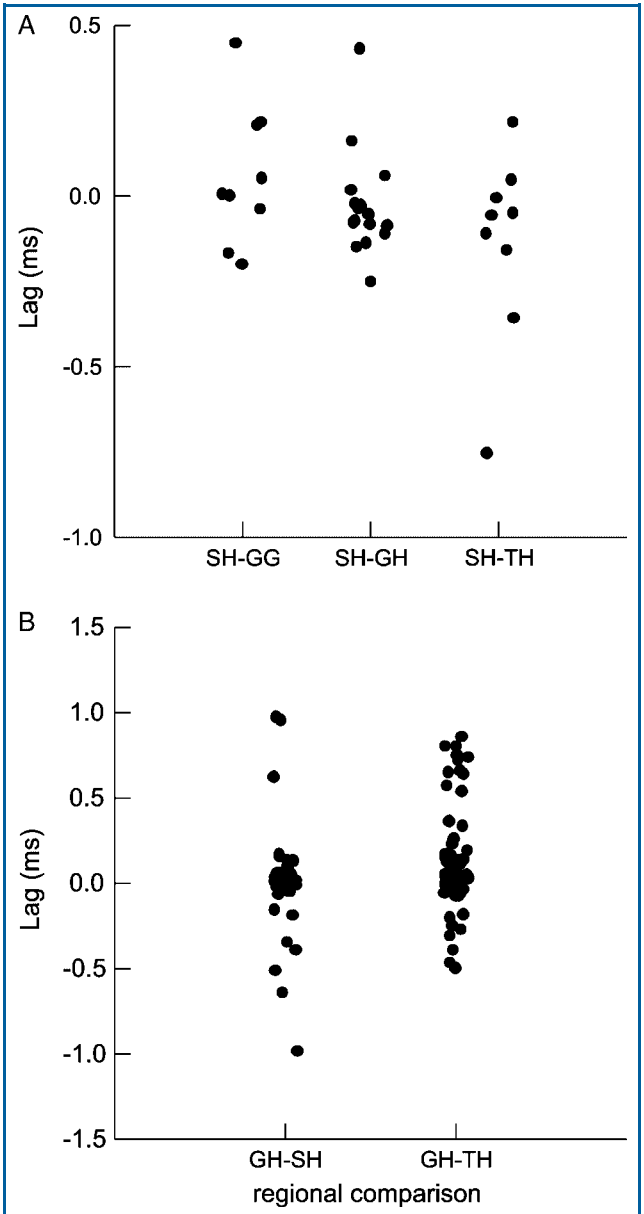

Figure 7. (A) Results of sternohyoid (SH) EMG compared with genioglossus, geniohyoid (GH), and thyrohyoid (TH) EMG. The EMG activity between SH to GG and SH to TH are statistically significant ($P < 0.001$ and $P = 0.007$), meaning there is a lag; however, the lag is clustered under 0.5 msec. The lag of SH to GH is not significant ($P = 0.82$). (B) Results of GH EMG compared with SH EMG and TH EMG. EMG activity between GH and SH is not different from zero ($P = 1.0$) and EMG activity between GH and TH does show statistically significant lag, though small ($P = 0.001$).

lengthening and shortening out-of-phase with the middle of the muscle. Shortening of the belly correlated with the muscle activity in this region, whereas the ends lengthened during muscle activity. Our interpretation of this pattern is that the muscle was being stretched as the head turns, and the belly was contracting eccentrically to resist this turn and to stabilize the hyoid bone against the pull of the muscles.

For the GH, strains in the belly and posterior regions were out-of-phase, whereas strain in the anterior region was in-phase with one or the other of these regions. Given that the length change in the belly and posterior regions are out-of-phase with each other, if the anterior region is in-phase with one region it will be out-of- phase with the other. There are two potential interpretations of this pattern. First, the anterior region of the GH could be truly random in its behavior with respect to its time relationship with the other regions. Sometimes, it could be contracting isontoically and other times actively lengthening or even being stretched by the head turn. Without fluoroscopic visualization, this is hard to resolve. Alternatively, it could be that we are not measuring the "functional units" within this muscle. That is, the end plates of the portion of the anterior region that is most consistently out-of-phase with the middle were not aligned with the crystals measuring length change. With more crystals, and histologically guided divisions of the GH, more exact length change phase relationships between the regions could be resolved. It follows that with our larger divisions, the observed length change could sometimes be dominated by a lengthening pool of motor units and sometimes by a shortening. The existence of multiple pools of motor neurons in the GH is already well documented (van Lunteren and Dick, 2000; German et al., 2009; Thexton et al., 2009).

The timing of changes in regional muscle length was characterized by a high level of variation for all regions in both muscles, complicating the interpretation of these results. For SH and GH, the large variation (Figs. 5 and 9) has an average lag, in most cases near zero.

Head Movement Including Shaking

Our results are consistent with some previous studies (Thompson, '41; Thompson and Brodie, '42; Forsberg et al., '85), but not all (Berzin, '95). Previously, head shaking has only been described in cats (Richmond et al., '92). The cat head shakes consisted of 1–5 rapid oscillations, usually completed in 100–150 msec and involving fast alternating movements from one side of the midline to the other. The EMG recordings for cat head shakes showed large bursts of activity for all the paravertebral muscles (Richmond et al., '92). We found similar large bursts for all of the hyoid musculature under study (Fig. 3A). These findings also support previous research by Forsberg et al. ('85). Using bipolar surface electrodes attached to the skin of the subject, Forsberg et al. ('85) found variation in EMG activity of both the infra- and suprahyoids during different amounts of head extension and flexion (Forsberg et al., '85). Extension and 20° of flexion showed increased activity relative to 5 or 10° of flexion. Interestingly, our results contradict the findings of Berzin ('95), who used needle

Table 2. Results of *t*-tests for GH group.

Regions tested	CCF correlation	df	Mean lag (msec)	SD (msec)	*t*-Value	*P*-value
aGH-mGH	Positive	22	−12.25	5.97	−9.838	<0.001
aGH-mGH	Negative	18	1.19	2.65	1.953	0.067
aGH-pGH	Negative	55	−0.98	12.60	−0.584	0.561
aGH-pGH	Positive	42	6.37	7.59	5.501	<0.001
aGHemg-mGHemg	Positive	69	−0.05	0.34	−1.272	0.207
mGHemg-pGHemg	Positive	69	0.08	0.32	2.065	0.043
aGHemg-pGHemg	Positive	69	0.01	0.27	0.043	0.966
GHemg-SHemg	Positive	42	0.00	0.32	0.000	0.999
GHemg-THemg	Positive	69	0.13	0.32	3.483	0.001

*$P<0.05$; **$P<0.001$. H_o : mean lag = 0.

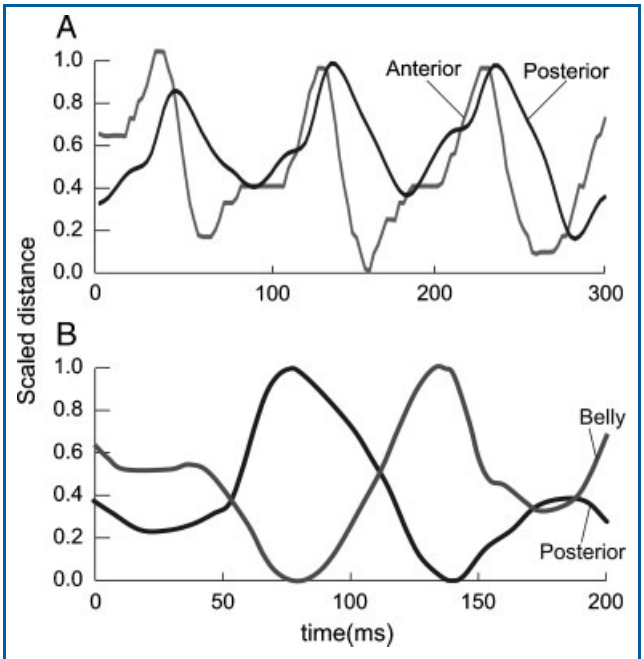

Figure 8. Regional strain heterogeneity in the geniohyoid. (A) Positive correlation, in-phase relationship, between anterior and posterior regions. Regions lengthen and shorten in synchrony, albeit with a lag. (B) Negative correlation between middle and posterior regions. One region lengthens, whereas the other shortens. Y-axis = scaled distance, X-axis = time (msec).

electrodes inserted into the human neck musculature and found the SH to be inactive during neck rotation, flexion, and extension movements (Berzin, '95).

Head shaking is a cyclical and rapid representation of a head turn. Based on our results, the hyoid musculature, and in particular the SH and GH muscles, seems to be active during such a movement. Clearly, kinesiology of the head is principally driven by the paravertebral and sternocleidomastoid muscles (Last, '55). The hyoid musculature is active in maintaining the posture of the head (Thompson, '41; Thompson and Brodie, '42), but the activity of the hyoid musculature during flexion, extension, and lateral movements of the head remains controversial (Brodie, '50; Forsberg et al., '85; Berzin, '95; Last, '95). Our study is consistent with Brodie ('50), Thompson ('41), and Forsberg et al. ('85), who found that the hyoid musculature shows motor activity during a head turn. Because our research involved regional length dynamics of the SH and GH, we not only quantified electrical activity, but also regional contraction specialization. The anterior to posterior gradient of muscle lengthening during a forceful behavior, such as a head shake, shows heterogeneity that is surprising for these simple muscles.

Head Shakes Compared With Swallowing

Some aspects of the complex regional differences in length change of SH and GH during head shakes mirror that of patterns in the SH during a more quiescent behavior, namely swallowing. The strain patterns in the belly region were negatively correlated with the anterior and posterior regions in swallows occurring early during a feeding session, when the pigs were most hungry (Konow et al., 2010). The belly was contracting at a different time than the end regions of the muscle. During later swallows, when the animal was less hungry, there was a difference between the anterior and posterior regions, with a posterior to anterior delay in muscle lengthening (Konow et al., 2010). This is the opposite of the anterior to posterior delay seen in head shakes. These data suggest that the SH displays different lengthening/shortening patterns, depending on behavior. The shake behavior involves a more abrupt and intense movement of the head and neck than swallowing, and we speculate that the anterior to posterior delay represents a more immediate response of the anterior region of the muscle closest to the hyoid bone in order to stabilize it.

Similar to our head shake results, swallowing was homogeneous in EMG activity across the SH regions. In the swallowing data, length changes in the middle portion of the muscle showed

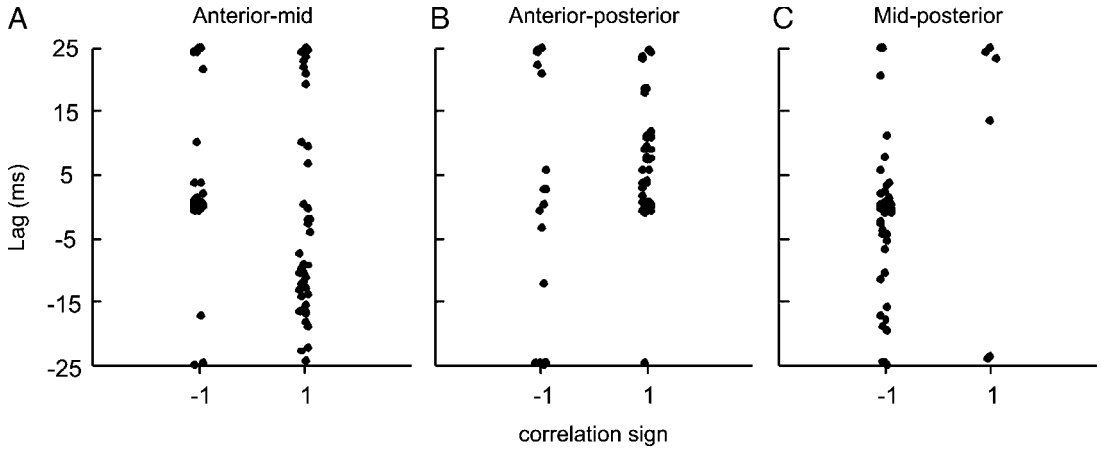

Figure 9. Results from analyses of geniohyoid regional strain. Each regional comparison produced a lag when negatively correlated (−1) and positively correlated (+1). (A) From the anterior to middle region, there is distribution across positive and negative correlations, showing that these regions have both strong "in-phase" and "out-of-phase" lengthening relationships. (B) The distribution of lags shows that from anterior to posterior, the regions are positively correlated (i.e. lengthening in-phase) and (C) the middle to posterior is mainly negatively correlated (i.e. out-of-phase).

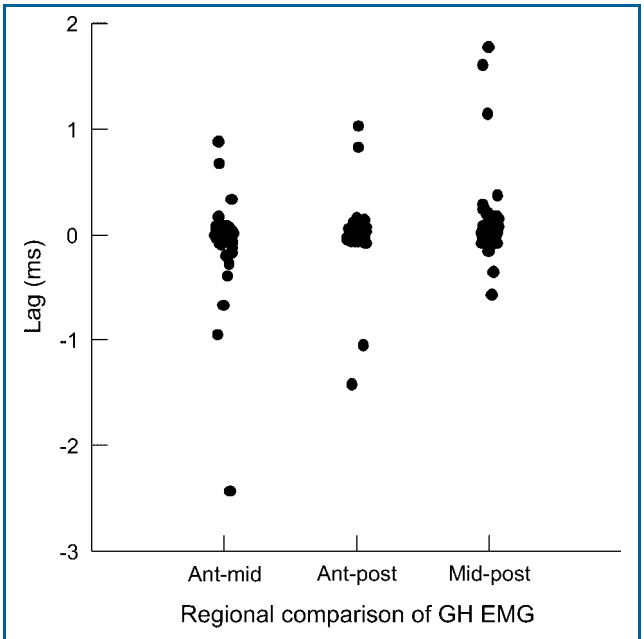

Figure 10. Results from analyses of geniohyoid regional EMG. All are positive correlations. Comparisons are: Ant-mid, anterior–middle ($P = 0.207$); Ant-post, anterior–posterior ($P = 0.966$); Midpost, middle–posterior ($P = 0.043$). $P > 0.05$ and, therefore, we accept H_o: mean lag = 0. The distribution shows points cluster at zero lag. GH shows interregional homogeneity in EMG activity.

the strongest relationship with peak EMG activity. The motor pattern does not seem to explain all of the dynamics and length changes of the muscle for either swallowing or head shaking behavior. The length of the SH results not only from its own contraction and relaxation, but also from the contraction and relaxation of its antagonists (i.e. suprahyoids). Therefore, the actions of this muscle include passive stretch and elastic recoil, in order to compensate for hyoid actuation by the suprahyoids, and the EMG patterns could be representative of these dynamics, and not pure relaxation/contraction.

The hyoid musculature is clearly very important during mammalian feeding behaviors and for stabilization of the hyoid bone (Smith, '92). Our understanding of the function and behavior of these muscles remains incomplete. Head shaking is a relatively simple reflex behavior, yet the patterns of muscle length dynamics and EMG activity are not. The regional heterogeneity of SH and GH strain during this behavior suggests that, despite their simple fusiform anatomy and non-differentiated nerve supply, these hyoid strap muscles are not characterized by the functional simplicity that textbooks often suggest.

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