Synchronization of presynaptic input to motor units of tongue, inspiratory intercostal, and diaphragm muscles

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Rice A, Fuglevand AJ, Laine CM, Fregosi RF. Synchronization of presynaptic input to motor units of tongue, inspiratory intercostal, and diaphragm muscles. J Neurophysiol 105: 2330–2336, 2011. First published February 9, 2011; doi:10.1152/jn.01078.2010.—The respiratory central pattern generator distributes rhythmic excitatory input to phrenic, intercostal, and hypoglossal premotor neurons. The degree to which this input shapes motor neuron activity can vary across respiratory muscles and motor neuron pools. We evaluated the extent to which respiratory drive synchronizes the activation of motor unit pairs in tongue (genioglossus, hyoglossus) and chest-wall (diaphragm, external intercostals) muscles using coherence analysis. This is a frequency domain technique, which characterizes the frequency and relative strength of neural inputs that are common to each of the recorded motor units. We also examined coherence across the two tongue muscles, as our previous work shows that, despite being antagonists, they are strongly coactivated during the inspiratory phase, suggesting that excitatory input from the premotor neurons is distributed broadly throughout the hypoglossal motoneuron pool. All motor unit pairs showed highly correlated activity in the low-frequency range (1–8 Hz), reflecting the fundamental respiratory frequency and its harmonics. Coherence of motor unit pairs recorded either within or across the tongue muscles was similar, consistent with broadly distributed premotor input to the hypoglossal motoneuron pool. Interestingly, motor units from diaphragm and external intercostal muscles showed significantly higher coherence across the 10–20-Hz bandwidth than tongue-muscle units. We propose that the lower coherence in tongue-muscle motor units over this range reflects a larger constellation of presynaptic inputs, which collectively lead to a reduction in the coherence between hypoglossal motoneurons in this frequency band. This, in turn, may reflect the relative simplicity of the respiratory drive to the diaphragm and intercostal muscles, compared with the greater diversity of functions fulfilled by muscles of the tongue.

METHODS

Experimental preparation. Studies were done in 61 male Sprague-Dawley rats weighing between 300 and 400 g, and all procedures were approved by the IACUC of The University of Arizona. Anesthesia was initiated by placing animals in a Plexiglas chamber gassed with discharges (Funk and Parkis 2002; Huang et al. 1993; Huang et al. 1996; Parkis et al. 2003; Peever et al. 2002; Sebe and Berger 2008; van Brederode and Berger 2008).

Most studies of synchronous oscillatory activity in respiratory muscle motoneurons have utilized recordings of left- and right-muscle nerves from hypoglossal, intercostal, or diaphragm motoneuron pools. These recordings provide useful information on the presynaptic modulation of an entire motoneuron pool but do not provide insight into the presynaptic control of identified muscles or features of the presynaptic input that is shared by pairs of motoneurons. For example, each hypoglossal nerve contains the axons of motoneurons innervating seven different tongue muscles, each with different mechanical actions and therefore different force and motor unit recruitment requirements. Similarly, intercostal nerves contain axons that innervate muscles with both inspiratory (external intercostals) and expiratory actions on the thorax (internal intercostals and triangularis sterni). Coherence analysis is a method that examines the correlation between two spike trains but in the frequency domain rather than the time domain. It provides an index of the strength of in-phase (i.e., synchronous) oscillations at each frequency examined. Because the method used to compute coherence removes the autospectra of the individual spike trains, in-phase oscillations that are common to each of the neurons are widely believed to reflect presynaptic inputs (Farmer et al. 1993; Farmer et al. 1997; Felliou et al. 2003; Felliou and Sejnowski 2000; Felliou et al. 2004; Kriener et al. 2008; Sejnowski and Paulsen 2006; Tetzlafl et al. 2008) (and see Discussion). Whether the nature of the presynaptic input to hypoglossal or intercostal motoneurons varies across the specific muscles controlled by these motoneuron pools is unknown.

Accordingly, the goal of this study is to examine the nature of the respiration-related presynaptic input that is shared by motor unit pairs in external intercostal muscles, the diaphragm, and two identified tongue muscles (the genioglossus and hyoglossus) with opposing mechanical actions. Comparisons were made within muscles (i.e., recording of two motor units from the same muscle) and also across the genioglossus and hyoglossus muscles (i.e., one motor unit from the genioglossus muscle, one motor unit from the hyoglossus muscle). This approach provided novel information on the composition and distribution of respiration-related presynaptic inputs driving identified muscle motoneuron pools.

INSPIRATORY MUSCLES OF THE THORAX (e.g., diaphragm, external intercostal muscles) and upper airway (e.g., tongue, pharyngeal, and laryngeal muscles) are driven by motoneurons that generate bursts of action potentials during the inspiratory phase of the respiratory cycle, with no or little activity during the expiratory phase. These bursts of activity are driven by long-duration (15–50 Hz) and high-frequency (50–120 Hz) ranges have been widely reported in pairs of inspiratory muscle motoneurons and in brainstem interneurons with both inspiratory and expiratory
3% halothane in oxygen. After induction, the animal was removed from the chamber but received the same anesthetic mixture via a nose cone. A polyethylene catheter was inserted into a femoral vein for the administration of drugs and fluids. As previously described (Bailey et al. 2001; Fuller et al. 1998; Fuller and Fregosi 2000; Fuller et al. 1999), the isoflurane dose was progressively reduced in exchange for deep urethane anesthesia administered intravenously to a final concentration of 1.3 g/kg, with anesthetic depth monitored by applying deep pressure to the paws. Supplemental doses (0.25 g/kg) of urethane were given as needed to maintain analgesia. Colonic temperature was monitored and maintained between 37 and 38°C with a thermprobe and temperature sensor connected to a servo-controlled heating pad. The genioglossus, hyoglossus, external intercostal, and diaphragm muscles were surgically exposed but left intact, as described previously (Bailey et al. 2001; Fuller et al. 1998; Fuller and Fregosi 2000; Fuller et al. 1999; Janssen and Fregosi 2000).

Electrophysiology. Motor unit potentials were recorded with high-impedance (10 MΩ) tungsten electrodes (Frederick Haer, Bowdoin, ME) and were differentially amplified (model 7WU16K; Grass Instruments, West Warwick, RI), filtered between 300 and 10,000 Hz, and monitored on a storage oscilloscope and computer screen (John et al. 2005). Amplifier output of the filtered motor unit action potentials were sent to an analog-to-digital converter, which sampled each channel at 20,000 Hz, with all data written to the hard drive of the computer and subsequently backed up on CD ROM discs.

In all experiments, two microelectrodes were inserted into a single muscle using micromanipulators (Narishige, Tokyo, Japan) to study within-muscle events or into each of two different muscles to examine across-muscle events. On the basis of several years of experience with these muscles in the rat model, we have learned to limit the penetration of the microelectrodes to distances that are less than the thickness of the muscle (John et al. 2005). Once we identified consistent discharge from two motor units on both electrodes (see Fig. 1), a 10–15-min recording period commenced. We then moved one or both electrodes to record from a presumptively different motor unit pair, and the protocol was repeated. We conducted postmortem analysis at the conclusion of six experiments to confirm electrode placement within the targeted muscle.

Motor unit discrimination. Motor unit potentials (Fig. 1) were discriminated on the basis of waveform shape and amplitude (Spike II software; Cambridge Electronic Design, Cambridge, UK), as described previously (John et al. 2005). In the urethane-anesthetized rat, the bursts of activity recorded from the tongue, diaphragm, and intercostal muscles are purely inspiratory (Bailey and Fregosi 2004; 2006; Bailey et al. 2005; Bailey et al. 2001; Fuller et al. 1998; Janssen and Fregosi 2000; Janssen et al. 2000). To compute discharge rate we calculated the inverse of the mean interspike interval of all action potentials generated during each burst, and then averaged across 20 such bursts for each motor unit. To obtain an estimate of discharge rate variability, we computed the coefficient of variation of the interspike intervals for each motor unit. This was done by dividing the standard deviation of the interspike interval by the average interspike interval for that unit and expressing the data as a percentage. Cycles containing nonrespiratory behaviors such as swallows or sighs, which are easy to identify because they cause obvious changes in discharge as well as prolongation of the expiratory period (Janssen et al. 2000), were excluded from analysis.

Coherence analysis. Coherence analysis is a frequency-domain technique that is commonly applied to dual motor unit recordings to reveal the frequency of oscillations that are common to each of the motor units (Farmer et al. 1993; Farmer et al. 1997; Myers et al. 2004). Computation of the coherence function produces a dimensionless number between 0 and 1, which reflects the strength of the correlation between the activities of the two actively discharging motor units at each frequency. Spike times of each unit were transformed into a continuous signal (sampling rate 1,000 Hz) with each spike represented as a 1-ms pulse. The coherence between two spike trains was calculated with Matlab software using unweighted, nonoverlapping data segments 2,048 ms in length, resulting in a frequency resolution of 0.49 Hz. These data were used to compute the magnitude-squared coherence at each 0.49-Hz interval over a frequency range of 0–500 Hz. However, because we found no evidence of coherent discharge at frequencies above 50 Hz, we focus on the 0–50-Hz frequency range.

Statistical evaluation of coherence was done in two ways. First, we analyzed the proportion of motor unit pairs showing significant coherence at each frequency between 0 and 50 Hz. To do this, we first obtained the 95% confidence level for each motor unit pair according to the equation \(1 - 0.05^\left(\frac{1}{N(N - 1)}\right)\) where \(N\) is the number of disjoint time segments used in the coherence estimation (Amjad et al. 1989; Rosenberg et al. 1989). We then derived the proportion of motor unit pairs showing significant coherence at each frequency and subsequently compared this result both within and across muscles using the \(\chi^2\)-test, followed by post hoc comparisons with Fisher’s exact test.

Second, the magnitude-squared coherence for all motor unit pairs was derived by converting raw coherence values into Z-scores using Fisher’s transform \(z = \text{atanh}(\sqrt{C})\), where \(C\) represents the magnitude-squared coherence; for simplicity, in the remainder of the article, magnitude-squared coherence is referred to as coherence magnitude. The Z-scores for each motor unit pair were then averaged across 2-Hz bins, and a one-way ANOVA was used to compare the values in each frequency bin. Two-tailed, unequal variance t-tests were used for pair-wise post hoc comparisons. Finally, for each motor unit pair, the maximum unbinned Z-value was calculated for the 10–20-Hz frequency band to test for correlation between coherence and the geometric mean firing rate of each motor unit pair.

RESULTS

Number of motor unit pairs and average motor unit discharge rates. We recorded the activity of 167 motor unit pairs from 61 animals. Within-muscle comparisons included recordings from 33 genioglossus motor unit pairs, 54 hyoglossus pairs, 14 external intercostal muscle pairs, and 13 diaphragm motor unit pairs. We also studied 22 hyoglossus-genioglossus pairs. We used an average of 7,344 ± 5,690 (mean ± SD) spikes from each motor unit to construct the coherence spectra. The average breathing frequency across all animals ranged from ~80 to 100 cycles per minute (93.81 ± 20.31, mean ± SD), or 1.33 to 1.66 Hz, consistent with findings reported previously in spontaneously-breathing, urethane-anesthetized rats (Bailey and Fregosi 2004; Bailey et al. 2006; Bailey et al. 2005; Bailey...
age inspiratory-related discharge rates (means characterized by high signal-to-noise ratios (see Fig. 1). Aver-
sistent, inspiratory-related activity, and all recordings were

For all muscles, single-motor unit activities exhibited con-
sistent, inspiratory-related activity, and all recordings were
characterized by high signal-to-noise ratios (see Fig. 1). Aver-
age inspiratory-related discharge rates (means ± SD) were
42.3 ± 7.9 Hz (N = 78), 52.3 ± 11.6 Hz (N = 128), 36.8 ±
7.8 Hz (N = 30), and 31.5 ± 6.1 Hz (N = 32) for genioglossus,
hyoglossus, intercostal, and diaphragm motor units, respec-
tively. One-way ANOVA revealed significant differences in
inspiratory-related discharge rate (F = 53.65, P < 0.001) with
hyoglossus > genioglossus > intercostal and diaphragm (all
P < 0.001 by Bonferroni post hoc tests).

Discharge-rate variability. We determined within-muscle
discharge-rate variability by computing the coefficient of vari-
ation of the interspike intervals (ISI) for all motor units (Fig. 2).
ANOVA revealed significant differences (F = 24.21, P =
0.0018) between the diaphragm and genioglossus (P < 0.001),
diaphragm and hyoglossus (P < 0.001), and diaphragm and
external intercostal muscles (P < 0.001); however, there were
no differences between intercostal and either genioglossus or
hyoglossus muscles, or between genioglossus and hyoglossus
muscles.

Coherence of motor units within a muscle. Simultaneous
recordings of two motor units within a muscle allowed us to
determine the proportion of the motor unit pairs of the muscle
that show coherent discharge at each frequency from 0–50 Hz
(Fig. 3A). For all four muscles, the proportion of coherent
motor unit pairs was very high at low frequencies and fell
monotonically from ~8–50 Hz. The curves for intercostal and
diaphragm muscle motor units were right shifted compared
with the tongue-muscle curves, such that the frequency at
which 50% of the motor unit pairs showed significant coher-
cence was 12 and 15 Hz for genioglossus and hyoglossus vs. 23
and 30 Hz for the intercostal and diaphragm-muscle motor
units.

Average coherence magnitudes for motor unit pairs recorded
within a muscle are shown over the 0–50-Hz frequency range
in Fig. 3B. Note that all muscles showed very high coherence
values over the 1–8-Hz bandwidth, reflecting the fundamental
respiratory burst frequency and the first three–four harmonics
of that frequency, as shown by analysis of the power spectra of
individual motor units (see representative examples in Fig. 4).

The average coherence magnitude of motor unit pairs from
each of the four muscles was compared statistically by con-
verting raw coherence values to Z-scores followed by one-way
ANOVA (see METHODS), and the results are provided in Fig. 3B,
bottom. ANOVA revealed systematic and highly significant
differences throughout the 10–20-Hz frequency band, whereas
post hoc analyses confirm that the 10–20-Hz differences were
dominated by contrasts between tongue and chest-wall mus-
cles.

Coherence of motor units across the genioglossus and hyo-
glossus muscles. The proportion of genioglossus-hyoglossus
motor unit pairs showing significant coherence at each fre-
quency is shown in Fig. 5A. As for the within-muscle compar-
isons shown in Fig. 3A, the proportion of coherent motor unit
pairs across the genioglossus and hyoglossus muscles was very
high at low frequencies but in this case fell more sharply. The
frequency at which 50% of the motor unit pairs showed
significant coherence was in the range of 9–11 Hz. Coherence
magnitude between hyoglossus and genioglossus muscle motor
units falls off very sharply at frequencies above 8 Hz, suggest-
ing that almost all of the coherent synchronization of motor
units in the genioglossus and hyoglossus muscles arises in the
respiratory central pattern generator (Fig. 5B).

Coherence: comparison of tongue muscles with muscles of
the chest wall. We combined all motor unit pairs recorded
within each of the tongue muscles and all motor unit pairs
recorded within each of the chest wall muscles to assess
differences in motor unit coherence between spinal and cranial
motoneurons (Fig. 6). Motor units of chest-wall muscles are
more likely to show coherent oscillations than are tongue-
muscle motor units over the 10–40-Hz bandwidth (Fig. 6A). The frequency where 50% of the pairs showed significant coherence was about 13 Hz for tongue-muscle motor units and 26 Hz for motor units from the chest-wall muscles. Significant differences in coherence magnitude between tongue and chest-wall motor units were detected in the 3–5-Hz and 10–20-Hz bandwidths, with chest-wall motor unit pairs exhibiting significantly higher coherence values than tongue-muscle motor unit pairs (Fig. 6B). Because previous studies in limb muscles show that the computation of coherence can be influenced by discharge rate (Christou et al. 2007; Lowery and Erim 2005), we examined the relationship between coherence magnitude and firing rate for all motor unit pairs by transforming coherence into Fisher’s $Z$-scores, computing the geometric mean discharge rate for each pair of motor units, and performing a Pearson-correlation analysis. As shown in Fig. 7, the relationship between coherence and discharge rate is flat ($r^2 = 0.00010$).

Because we did not measure blood gases in our experiments, it is possible that changing anesthetic levels and thus blood gases, both within and across experiments, may have biased our results. Accordingly, for each pair of motor units studied,
we measured the animal’s respiratory frequency as an index of anesthetic depth and computed the correlation between the magnitude-squared coherence of each motor unit pair and the respiratory frequency. The results of this analysis show no relationship between breathing rate and coherence in the 10–20-Hz range ($r^2 = 0.0008$, $P = 0.76$). In addition, to insure that there were no systematic differences in anesthetic depth during recordings of chest-wall-muscle and tongue-muscle motor unit pairs, we compared the average breathing frequency associated with all recordings of diaphragm, intercostal, hyoglossus, and genioglossus motor unit pairs. The results of this analysis also revealed no significant differences ($F = 0.169$, $P = 0.174$).

**DISCUSSION**

Summary. Phasically driven motor units in muscles of the tongue and chest wall show strong correlated activity at frequencies between $\sim 1.5$ and 8 Hz. Coherence at these low frequencies represents synchronized presynaptic oscillations at the fundamental frequency of the respiratory central pattern generator and harmonics of this fundamental frequency. These observations were expected; as in our preparation the motor units are driven spontaneously by an exceptionally strong, stereotyped input function that is distributed concurrently to spinal (intercostal, diaphragm) and cranial (tongue muscles) motoneurons. Although there were small differences in the coherence profiles of tongue vs. chest-wall motor units in the 3–5-Hz range, the largest and most consistent differences were between about 10 and 20 Hz, with chest-wall-muscle motor units showing higher levels of coherence throughout this frequency band. We propose that the lower coherence in tongue-muscle motor units over this range reflects a larger constellation of presynaptic inputs, which collectively lead to a reduction in the coherence between hypoglossal motoneurons in this frequency band. This, in turn, may reflect the relative simplicity of the respiratory drive to the diaphragm and intercostal muscles, compared with the greater diversity of functions fulfilled by muscles of the tongue.

Motor unit discharge rates and variability. Tongue-muscle motor units had significantly higher discharge rates than the two chest-wall muscles, with the hyoglossus muscle having the highest of all and the diaphragm the lowest. This is consistent with recent data in human subjects, showing rates of 10–18 Hz in diaphragm, 8–11 Hz in external intercostal muscles, and 14–30 Hz in the genioglossus muscle (Saboisky et al. 2007a; Saboisky et al. 2007b). In adult rats, the input resistance of phrenic and hypoglossal motoneurons is about 2 and 12 Mohms, respectively (Hayashi and Fukuda 1995; Viana et al. 1995). Similarly, rheobase current ranges from 5–14 nA in phrenic motoneurons (Jodkowski et al. 1987) and 1–2 nA in hypoglossal motoneurons (Takata et al. 1980). Thus equivalent levels of synaptic input should result in higher discharge rates in hypoglossal motoneurons, as they are intrinsically more excitable.

Interestingly, the coefficient of variation of motor unit discharge rates is also significantly lower in the diaphragm compared with the other muscles. Given that the variability of interspike intervals increases as a function of the amplitude and frequency content of synaptic noise and the duration of the afterhyperpolarization current (Powers et al. 2002), this observation is consistent with increased synaptic noise and/or different intrinsic motoneuron properties in tongue compared with diaphragm muscles. Taken together, these observations suggest that motor units with lower intrinsic excitability have slower and more uniform firing profiles. Interestingly, using our average firing rate data together with published data on the proportion of type I muscle fibers for each of the muscles yields an inverse, monotonic relationship (Fig. 8). It is noteworthy that the tongue muscles have either no type I fibers (hyoglossus) or just a few (genioglossus) inasmuch as histochemical fiber type correlates with muscle-shortening velocity, axon diameter, and input resistance (Sawczuk et al. 1995). This relationship is expected but is consistent with the significant differences in firing rates in the tongue and chest-wall muscles that we observed here.

Coherence of motor units within a muscle. Previous studies have examined the correlated discharge of pairs of motor units during volitional contractions in human subjects and used coherence analysis to estimate the extent to which in-phase oscillations synchronize motoneuron discharge (Baker et al. 1999; Farmer et al. 1997; Laine and Bailey 2011; Lowery et al. 2007). Similarly, in vitro studies have shown that in-phase oscillations in the 20–50-Hz range are involved in spike-timing precision in phrenic motoneurons (Parkis et al. 2003) and that the reliability of action potential discharge in hypoglossal motoneurons is highest when the input frequency of an injected sinusoid is in the 3–25-Hz range (van Brederode and Berger 2008). Our data are consistent with these observations inasmuch as the frequency at which 50% of the motor unit pairs showed significant coherence is about 13 and 26 Hz for tongue and chest-wall muscles, respectively (Fig. 6A). However, we have also demonstrated that the incidence and magnitude of inspiratory-phase coherence in the 10–20-Hz bandwidth is consistently and significantly greater in muscles of the chest wall compared with muscles of the tongue (Fig. 6, A and B).

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**Fig. 7.** Coherence magnitude (transformed into Fisher’s Z-scores) as a function of discharge rate for all motor unit pairs studied. The mean discharge rate was computed as the geometric mean of the average discharge rate of each motor unit in a pair. The regression line and $r^2$ values are shown.

**Fig. 8.** Relationship between the average discharge rate that we recorded in rodent hypoglossus, genioglossus external intercostal, and diaphragm muscles and the percentage of type I muscle fibers in each muscle, as reported by others (Cunningham et al. 1991; LaFramboise et al. 1992; Prakash et al. 2000; Smith et al. 2005; Sutlive et al. 2000).
motor units. Although the reason for this difference is unknown, it is clear that statistically significant coherence in this frequency band would require a reasonably strong in-phase oscillation that is common to each of the motor units being analyzed. However, if one motoneuron pool receives more sources of input that contain activity in the 10–20-Hz range, and if those inputs arrive out of phase with each other, they will summate destructively, leading to relatively weaker coherence. On the basis of this idea, we suggest that, in addition to the inputs from the respiratory central pattern generator that appear to be shared equally by both motoneuron pools, the hypoglossal motoneurons receive a wider constellation of presynaptic inputs than phrenic/intercostal motoneurons, possibly attributable to the wider range of functions performed by tongue muscles compared with diaphragm or intercostal muscles. Some evidence for this conclusion includes robust, inspiratory-phase GABAergic and glycinergic inputs to hypoglossal motoneurons from the reticular formation (Fenik et al. 2004; Fenik et al. 2005; O’Brien et al. 2004; Remmers et al. 1980; Withington-Wray et al. 1988; Woch and Kubin 1995) and also the nucleus of the Roller (Marchetti et al. 2002; O’Brien et al. 2004), which is a relay site for sensory afferents. Importantly, our previous work in the same preparation showed that pulmonary stretch receptors evoke much stronger inhibition of tongue compared with intercostal muscles (Bailey et al. 2001; Fregosi and Fuller 1997; Janssen et al. 2000), consistent with stronger inhibitory synaptic inputs to hypoglossal compared with intercostal motoneurons.

Coherence between genioglossus and hyoglossus muscle motor units. In the last decade, our laboratory has documented respiratory-related coactivation of protruder and retractor tongue muscles in the rat (Bailey and Fregosi 2004; Bailey et al. 2001, 2005; Fuller et al. 1998; Janssen and Fregosi 2000; Janssen et al. 2000), observations that were subsequently confirmed in human subjects (Mateika et al. 1999). The present results show very low coherence at frequencies above those that are due to the fundamental respiratory frequency and the first few harmonics of this fundamental frequency. These results suggest that presynaptic input from the central pattern generator is distributed broadly to the hypoglossal premotor neuron pool, leading to synchronized excitation of hypoglossal motoneurons that drive both protruder and retractor muscles of the tongue. Previous anatomic studies have shown that motoneurons driving the genioglossus and hyoglossus muscles in the rat are somatotopically organized within the hypoglossal motor nucleus (Dobbins and Feldman 1995; Gilliam and Goldberg 1995; Guo et al. 1996; McClung and Goldberg 1999, 2000, 2002), but we do not know whether the hypoglossal premotor neurons that convey excitatory synaptic input from the respiratory central pattern generator have unique projections to genioglossus and hyoglossus motoneurons, or whether they branch extensively to innervate motoneurons in two or more muscle motoneuron pools. Peever et al. (2001) used cross-correlation analysis of inspiratory bursts in medial and lateral hypoglossal nerve branches (which innervate the genio- glossus and hyoglossus muscles, respectively) and found strongly correlated activity. In contrast, they failed to find significant correlations between hypoglossal and phrenic nerve activities. They interpreted the data as evidence for a common drive from the hypoglossal premotor neuron pool, which agrees with our findings of similar coherence profiles among genioglossus and hyoglossus motor units. These observations and the present ones suggest that excitatory synaptic input from the respiratory central pattern generator is distributed broadly to the hypoglossal premotor neurons, leading to respiratory-related coactivation of genioglossus and hyoglossus muscles.

Conclusions. Phasically driven motor units in muscles of the tongue and chest wall show strong correlated activity at frequencies between ~1.5 and 8 Hz, reflecting presynaptic oscillations from the respiratory central pattern generator and harmonics of this fundamental frequency. Chest-wall muscle motor units consistently showed higher levels of coherence than tongue muscle motor units over the 10–20-Hz frequency band. We propose that the lower coherence in tongue-muscle motor units over this range reflects a larger constellation of presynaptic inputs, which collectively lead to a reduction in the coherence between hypoglossal motoneurons in this frequency band. This, in turn, may reflect the relative simplicity of the respiratory drive to the diaphragm and intercostal muscles, compared with the greater diversity of functions fulfilled by muscles of the tongue.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

REFERENCES


A simulation study to examine the effect of common
Laine CM, Bailey EF.
Mateika JH, Millrood DL, Kim J, Rodriguez HP, Samara GJ.
Marchetti C, Pagnotta S, Donato R, Nistri A.
Kriener B, Tetzlaff T, Aertsen A, Diesmann M, Rotter S.
Jodkowski JS, Viana F, Dick TE, Berger AJ.
Janssen PL, Williams JS, Fregosi RF.
Fellous JM, Sejnowski TJ.
Fenik V, Davies RO, Kubin L.
Fenik V, Davies RO, Kubin L.
Guo Y, Goldberg SJ.
Huang WX, Cohen MI, Yu Q, See WR, He Q.
Huang WX, Cohen MI, Yu Q, See WR, He Q.
Janssen PL, Fregosi RF.
Jodkowski JS, Viana F, Dick TE, Berger AJ.
John J, Bailey EF, Fregosi RF.
Kriener B, Tetzlaff T, Aertsen A, Diesmann M, Rotter S.
Laframboise WA, Watchko JF, Brozanski BS, Daoed MJ, Guthrie RD.
Laine CM, Bailey EF.
Lowery MM, Erim Z.
Lowery MM, Myers LJ, Erim Z.
Marchetti C, Pagnotta S, Donato R, Nistri A.
Inhibition of spinal or hypoglycoidal motoneurons of the newborn rat by glycine or GABA. *Eur J Neurosci* 15: 975–983, 2002.
Mateika JH, Millrood DL, Kim J, Rodriguez HP, Samara GJ.
McClung JR, Goldberg SJ.
McClung JR, Goldberg SJ.
McClung JR, Goldberg SJ.
Myers LJ, Erim Z, Lowery MM.
O’Brien JA, Sebe JY, Berger AJ.
GABA(B) modulation of GABA(A) and glycine receptor-mediated synaptic currents in hypoglycoidal motoneurons. *Respir Physiol Neurobiol* 141: 35–45, 2004.
Parkis MA, Feldman JL, Robinson DM, Funk GD.
Peever JH, Duffin J.
Peever JH, Mateika JH, Duffin J.
Peever JH, Shen L, Duffin J.
Powers RK, Turker KS, Binder MD.
Prakash YS, Martilla CB, Zhan WZ, Smithson KG, Sieck GC.
Rosenberg JR, Anjard AM, Breeze P, Brillinger DR, Halliday DM.
Sabolsky JP, Butler JE, Walsh LD, Gandevia SC.
Sabolsky JP, Gorman RB, De Troyer A, Gandevia SC, Butler JE.
Sawczuk A, Powers RK, Binder MD.
Sebe JY, Berger AJ.
Sebe JY, van Brederode FJ, Berger AJ.
Sejnowski TJ, Paulsen O.
Smith JC, Goldberg SJ, Shalil MS.
Sutlive TG, Shalil MS, McClung JR, Goldberg SJ.
Takata M, Shohara E, Fujita S.
Tetzlaff T, Rotter S, Stark E, Abeles M, Aertsen A, Diesmann M.
van Brederode FJ, Berger AJ.
Viana F, Bayliss DA, Berger AJ.
Withington-Wray DJ, Milfin SW, Spyer KM.
Woch G, Kubin L.