Discharge Rate of Sternohyoid Motor Units Activated With Surface EMG Feedback

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Farina D, Falla D. Discharge rate of sternohyoid motor units activated with surface EMG feedback. J Neurophysiol 101: 624–632, 2009. First published November 26, 2008; doi:10.1152/jn.90901.2008. We analyzed individual motor units of the sternohyoid muscle with the aim of characterizing their minimum and maximum discharge rates and their variability in discharge during voluntary contractions. Surface EMG signals were recorded with an array of eight electrodes from the sternohyoid muscle of seven healthy men (age: 30.2 ± 3.5 yr). The multichannel surface EMG signals were displayed as feedback for the subjects who identified and modulated the activity of one target motor unit in 30-s contractions during which the discharge rate was increased from minimum to maximum (ramp contraction), sustained at maximum level (sustained), or increased in brief bursts (burst). During the ramp contractions, the minimum average discharge rate over epochs of 1 s was 11.6 ± 1.5 pulses per second (pps) and the maximum 57.0 ± 5.7 pps (P < 0.001). During the sustained contractions, the motor unit discharge rate decreased from 65.5 ± 8.4 pps at the beginning to 52.9 ± 7.6 pps at the end of the contraction (P < 0.05). The coefficient of variation for the interspike interval during the sustained contractions was 40.2 ± 9.8% and a large percentage of discharges had instantaneous rates >50 pps (52.2 ± 12.5%) and >100 pps (8.0 ± 1.2%), with peak values >150 pps. During the burst contractions, the instantaneous discharge rate reached average maximum values of 97.6 ± 36.8 pps. The observed discharge rates and their variability are higher than those reported for limb muscles, which may be due to large synaptic input and noise received by these motor neurons.

INTRODUCTION

The discharge characteristics of motor units have been described for several limb muscles. In these muscles, motor units discharge tonically at a minimum rate of approximately 6–10 pulses per second (pps) and reach stable rates of up to about 45 pps (Andreassen and Rosenfalck 1980; Duchateau and Hainaut 1990; Hockensmith et al. 2005; Kamen et al. 1995; Monster and Chan 1977). These maximal rates are usually lower than those required to achieve maximum tetanic force. For example, intraneural stimulation of single motor units indicates that the peak force for a motor unit is achieved at average rates close to 100 Hz (Fuglevand et al. 1999; Macefield et al. 1996; Thomas et al. 1991). Moreover, motor neurons may not respond to increased synaptic input after they reach their maximum rate (e.g., Johns and Fuglevand 2004). This mechanism, which is known as discharge rate saturation, seems to be a prominent and general feature of different types of muscles (Bailey et al. 2007; Johns and Fuglevand 2004; Monster and Chan 1977) and limits the maximum rates to relatively low values.

Single motor units can be easily investigated in limb muscles because of the possibility of inserting intramuscular electrodes with limited risk for the subject. However, there is less information on motor unit behavior for muscles that are more difficult to access with invasive techniques. Although many characteristics of motor unit behavior are similar across muscles, some differences are occasionally observed, especially in muscles with complex and highly specialized functions. For example, the average rate at which genioglossus motor units discharge tonically during a holding task with the tongue is higher than that reported for most limb motor units (Bailey et al. 2007). Moreover, genioglossus motor units may sporadically discharge in brief bursts with higher rates compared with limb muscles (Bailey et al. 2007). Thus although most of our knowledge on motor unit properties is based on recordings from limb muscles, some characteristics of motor unit behavior may vary across muscles. Differences with respect to classic control schemes may be expected for muscles with complex functions. For example, deglutition and phonation are tasks that imply very specific muscle control, which may require different motor unit activation with respect to limb muscles.

The submental muscles are important for hylolaryngeal excursion during swallowing due to their insertion on the hyoid bone. Contraction of these muscles during the pharyngeal stage of swallowing serves to move the hyoid bone and, subsequently, the larynx to allow airway protection and the opening of the upper esophageal sphincter (Cook et al. 1989; Dodds et al. 1990; Donner 1985). During swallowing, the suprahyoid muscles act to raise the hyoid bone and larynx, whereas the infrapharyoid muscles have the opposite action. These muscles are also rhythmically active during respiration (Rothstein et al. 1983). The suprahyoid muscles are innervated by motor neurons located in the trigeminal and facial nuclei in the pons, except for the genioglossus, which, as the infrapharyoid group, is innervated by motor neurons within the anterior horn of the upper cervical spinal cord. The electrical activity of the hyoid muscles has been investigated using surface electromyography (EMG) (Ding et al. 2002; Huckabee et al. 2005), although there are no reports on the discharge characteristics of motor units in these muscles.

In this study, we hypothesized that the very specialized function of the infrapharyoid muscles corresponds to different characteristics of motor unit behavior with respect to limb muscles, as reported for some motor unit properties in other muscles.
orofacial muscles (Bailey et al. 2007). Thus we analyzed the discharge characteristics in individual motor units of the sternohyoid muscle with the aim of characterizing the minimum and maximum discharge rates and their variability during voluntary contractions. Because it was not possible to measure force from this muscle, feedback on motor unit action potentials, instead of force, was provided to the subjects.

METHODS

Subjects

Eleven healthy men (age [mean ± SD], 28.7 ± 4.1 yr) participated in the study, although only seven (age, 30.2 ± 3.5 yr) were able to control a target motor unit using the surface EMG feedback (see RESULTS). The study was in accordance with the Declaration of Helsinki and approved by the local ethics committee (VN 2005/38). The subjects provided written informed consent before participation.

EMG recordings

Surface EMG signals were recorded with adhesive linear arrays of eight electrodes (1 × 5-mm size, 5-mm interelectrode distance) from the sternohyoid muscle unilaterally and from the sternocleidomastoid muscle bilaterally (Fig. 1). The sternohyoid muscle was initially assessed bilaterally during swallowing with a dry array of silver electrodes (1 × 5-mm size, 10-mm interelectrode distance) to identify an optimal location of the electrodes, whereas a standard location was used for the sternocleidomastoid muscle (Falla et al. 2002). The side that showed larger activity of the sternohyoid muscle during the swallowing test was selected for the investigation. Prior to placement of the adhesive arrays, the skin was lightly abraded with abrasive paste and cleansed with water. A ground electrode was placed around the right wrist.

The EMG signals were amplified (gain 10,000–20,000) with a multichannel surface EMG amplifier (LISiN; OT Bioelettronica, Turin, Italy), band-pass filtered (−3-dB bandwidth, 10–500 Hz), sampled at 2,048 samples/s, and converted to digital data by a 12-bit A/D converter board. The acquisition software provided real-time display of the seven bipolar signals recorded from the sternohyoid muscle.

Procedures

The subject was seated comfortably on a chair, knees and hips in 90° of flexion, with the head resting against a padded support. The surface arrays were mounted as described earlier; the correct placement over the sternohyoid muscle was confirmed by a few contractions performed during swallowing (Fig. 2) and by the presence of propagating action potentials along the array that excluded the possibility of crosstalk (Farina et al. 2002). The signals concurrently recorded from the sternocleidomastoid muscles were used to further exclude the possibility of crosstalk from the sternocleidomastoid. The subject was provided with on-line visual feedback of the EMG signals recorded from the sternohyoid and was asked to freely choose a strategy of activation of this muscle (e.g., jaw opening) to identify the activity of a single motor unit (target unit) in the surface EMG recordings. The bipolar surface EMG signals were displayed on-line on the monitor of a PC, located in front of the subject. Signals with poor signal-to-noise ratio were excluded from the feedback. The display presented 500-ms portions of signals (Farina et al. 2000a) and the gain was adjusted to optimize the quality of the feedback. The subject was given about 20 min to train with the feedback and in case he did not succeed in reliable identification of the activity of a single motor unit, the test was interrupted. If the subject could control the target unit using the feedback, he was asked to modulate the target motor unit discharge rate during three contractions, each of 30-s duration: 1) increased discharge rate from minimum to maximum (ramp contraction), 2) sustained maximum discharge rate (sustained), and 3) repetitive bursts of activity (−2-s rest in between) reaching the maximum instantaneous rate (burst). The order of these contractions was randomized. During these contractions, the subject was asked not to exceed a level of activation for which the action potentials of motor units other than the target unit substantially contributed to the surface EMG recording.

Signal analysis

Surface EMG signals were decomposed off-line to identify all discharges of the target motor unit (Gazzoni et al. 2004). The number of superimposed action potentials was negligible because of the feedback modality. Activation of the same motor unit during the entire duration of the contraction was ensured by the absence of sudden changes in action potential shape and the presence of a continuous discharge pattern. The possibility of concurrent activation of motor units different from that under analysis but with action potentials of similar shape and amplitude was excluded since this would have determined occasional superimpositions of action potentials from two or more motor units and thus large sudden changes in action potential amplitude, which was not observed (see RESULTS). The autocorrelation function of the series of interspike intervals (ISIs) was also computed to exclude the presence of discharges from two motor units. The possibility that the action potentials of the target motor unit were generated by cross talk from nearby muscles was analyzed by assessing the propagation properties of the action potentials along the array and by spike-triggered averaging of the signals recorded from the sternocleidomastoid muscle using the action potentials detected by the array on the sternohyoid as the trigger.

Instantaneous discharge rate was computed as the inverse of the ISI and the ISI variability was defined as the ratio (%) between SD and mean ISI. ISI variability was computed only for the sustained contractions because the average discharge rate varied rapidly in the other contraction types. The ISI variability during the sustained contractions was also analyzed by computing the correlation coefficient between the nth ISI and the (n + 1)th ISI (Berg et al. 2007). The comparison of discharge rates among contractions and between time intervals within the same contraction was performed with Student’s t-test, with a significance level of P < 0.05. Results are presented as means and SD.

RESULTS

Seven of the 11 subjects were able to identify one target unit in the three contraction types; thus the results presented refer to seven motor units activated in three contractions by seven
subjects. There were no other motor units, in addition to the target motor unit, significantly contributing to the surface EMG signal during the contractions with feedback. The presence of only the target unit was confirmed by the constant peak-to-peak amplitude of the recorded signal (e.g., Fig. 3A). The presence of two or more motor units with similar action potentials would have determined changes in the peak amplitude of the signal due to action potential superimpositions, however this was never observed. Moreover, the average absolute value of the autocorrelation function of the ISI for all time lags, excluding the peak value, was (over all subjects for the ramp and sustained contractions) 0.018 ± 0.013, which excluded the possibility that the series of ISIs was generated by more than one unit.

In all subjects and contractions, it was possible to identify at least two channels (range: 2–4 channels) of the array along which the action potentials showed propagation (e.g., Fig. 3B). The presence of propagating action potentials indicated that the signals were not generated by far sources (cross talk) (Dimitrova et al. 2002; Farina et al. 2002). Moreover, the spike-triggered average of the sternocleidomastoid muscle signals, using the detected potentials as a trigger, corresponded in all subjects to negligible peak-to-peak amplitude (average, 2.1 ± 1.1 μV) with respect to the amplitude of the trigger potentials detected on the sternohyoid muscle (153.2 ± 20.4 μV), which excluded the possibility of cross talk from the sternocleidomastoid muscle.

Figure 3 shows a representative ramp contraction. The subject maintained the target motor unit active for the duration of the contraction while increasing the discharge rate. The minimum average discharge rate (epochs of 1-s duration) during the ramp contractions was (mean ± SD, over all subjects) 11.6 ± 1.5 pps and the maximum 57.0 ± 5.7 pps ($P < 0.001$; Table 1). The subjects could modulate the discharge rate in this range with an approximately linear increase (Fig. 3C). In the results presented, the resolution in computing the ISI is 0.49 ms (for 2,048-Hz sampling frequency). For example, at 100 pps of instantaneous rate, the ISI is 10 ms and is estimated with a relative error of about 5% (0.49 ms of resolution divided by 10 ms). Thus for high discharge rates, slightly different rates are estimated as the same value. This limit in resolution does not affect the results presented.

Figure 4 shows a recording during a sustained contraction. In this representative contraction, more than half of the discharges occurred at <20-ms separation (Fig. 4C) and the instantaneous discharge rate reached about 150 pps (~7-ms separation between discharges). During the first second of activity in the sustained contractions, the average discharge rate for the investigated motor units was 65.5 ± 8.4 pps and decreased to 52.9 ± 7.6 pps at the end of the contraction (last second) ($P < 0.05$; Table 1). The discharge rate at the beginning of the sustained contractions was higher than the maximum discharge rate achieved during the ramp contractions ($P < 0.05$). The coefficient of variation (CV) of the ISI during the sustained contractions was 40.2 ± 9.8%, indicating high variability in the discharges. The high CV corresponded to a low correlation between the $n$th and ($n + 1$)th ISI ($R = 0.22 ± 0.06$). Repetitive consecutive discharges at instantaneous discharge rates >50 pps were observed in all subjects. The percentage of these discharges over all of the sustained contractions was 52.2 ± 12.5%, whereas the percentage of discharges with instantaneous rate >100 pps was 8.0 ± 1.2%. These values were in agreement with the theoretical predictions obtained by assuming a Gaussian distribution of the ISIs with the observed mean and SD values for ISI. For example, for a mean discharge rate of 55 pps (18.2-ms ISI) and a CV for the ISI of 40%, the theoretical expectations for percentage of discharges with ISIs <20 ms (50 pps) and <10 ms (100 pps) are 59.4 and 12.3%, respectively, similar to the observed values. In one subject the maximum average discharge rate at the beginning of the sustained contraction reached about 80 pps and decreased to about 60 pps at the end of the contraction (Fig. 5A). In this subject the instantaneous discharge rate reached about 180 pps (~5-ms separation between action potentials) and the percentages of discharges with instantaneous rate >50 and >100 pps were 62.7 and 8.5%, respectively. In many cases, bursts of several consecutive action potentials each at a distance <20 ms from the next, were observed (Figs. 4D and 5B).

Figure 6 shows one contraction with bursts of activation. The average duration of the bursts of activity (from the first to the last action potential in the burst) was 550 ± 98 ms. The discharge rate at the beginning of each burst was very high, although the discharge rate decreased rapidly during the bursts (Fig. 6). In the subject represented in Fig. 6, the instantaneous discharge rate reached a maximum of close to 170 pps, as in some of the sustained contractions. On average, the maximum discharge rate reached during the burst contractions was 97.6 ± 36.8 pps (Table 1).

**DISCUSSION**

This study is the first that characterizes the discharge rate of motor units in the sternohyoid muscle during voluntary activation with feedback on motor unit action potentials. The subjects could modulate the discharge rate of these motor units over a large range of values and the maximal discharge rates achieved were higher than those previously observed in limb muscles (Monster and Chan 1977).

Because the detected action potentials propagated along the direction of the array, it was assumed that they were generated
by the sternohyoid muscle, directly beneath the array. Although this interpretation is the most likely, the limited selectivity of surface EMG recordings does not allow precise identification of source locations. Nevertheless, the verification of absence of cross talk from the sternocleidomastoid muscle implies that the recorded electrical activities were certainly generated by one of the infrahyoid muscles, which are very close to each other, and most likely by the sternohyoid, which has the largest superficial area and was located directly beneath the array.

The motor units were analyzed by providing the subjects with visual feedback on the detected multichannel surface EMG. This method was previously applied to hand (Farina et al. 2004a; Gazzoni et al. 2005) and neck (Farina and Falla 2008) muscles. The subjects could modulate the intensity of muscle activity without feedback on force, which could not be measured from this muscle. The motor unit discharge rates observed using this technique in other muscles were within the range usually reported in force-feedback contractions (Farina and Falla 2008; Farina et al. 2004a; Gazzoni et al. 2005). In the current study, the feedback on surface EMG allowed 7 of the 11 subjects investigated to control individual motor units. The limited selectivity of surface EMG and the dependence of signal quality on anatomical factors, such as the thickness of subcutaneous layers (Farina et al. 2004b), were the likely reasons for the inability to use surface EMG visual feedback in these 4 subjects. Three of the 4 subjects excluded from the analysis could use the feedback and identified a target motor unit that

**TABLE 1.** Discharge rates (pps) observed for the motor units in the sternohyoid muscle in seven subjects

<table>
<thead>
<tr>
<th>Subject</th>
<th>Ramp</th>
<th>Sustained</th>
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<td>Sustained</td>
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<tr>
<td></td>
<td>Beginning*</td>
<td>End*</td>
<td>Beginning*</td>
<td>End*</td>
<td>Burst Max**</td>
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<td>63.7</td>
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<td></td>
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<tr>
<td>3</td>
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<td>63.3</td>
<td>64.3</td>
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</tr>
<tr>
<td>4</td>
<td>11.4</td>
<td>61.4</td>
<td>57.5</td>
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<tr>
<td>5</td>
<td>11.4</td>
<td>51.6</td>
<td>67.2</td>
<td>53.8</td>
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<td></td>
</tr>
<tr>
<td>6</td>
<td>9.2</td>
<td>48.3</td>
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<td>43.5</td>
<td>75.8</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>12.4</td>
<td>54.9</td>
<td>67.1</td>
<td>53.2</td>
<td>85.3</td>
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</table>

*Average over 1-s epoch duration. **Maximum instantaneous rate.
could be controlled at low discharge rates. However, in these subjects, the surface EMG recordings were not sufficiently selective when the intensity of activity was increased; thus the action potentials of the target motor unit could not be discriminated with sufficient accuracy. The subjects selected for the final analysis were those with highly selective recordings (e.g., Figs. 3–6), to be confident that the action potentials of one single unit could be discriminated with a high degree of certainty.

The seven subjects included could identify the action potentials of the target motor unit for a large range of discharge rates. During these contractions, the subjects were asked to decrease the intensity of activation if they observed action potentials of motor units other than the target unit. It is likely that many other units were active during the contractions with feedback, although their action potentials did not contribute to the recorded surface EMG.

The average rate at which sternohyoid motor units were found to discharge tonically (minimum discharge rate during the ramp contractions) was higher than those reported for most limb motor units, which typically discharge at 6–10 pps (Andreassen and Rosenfalck 1980; Hockensmith et al. 2005; Monster and Chan 1977). Because the minimum discharge rate is inversely related to the duration of the afterhyperpolarization (AHP) following the action potential (Kernell 1965), sternohyoid motoneurons may have shorter periods of AHPs with respect to neurons innervating limb muscles. Interestingly, genioglossus motor neurons have also been reported to discharge at a minimum rate higher than that of limb motor units (Bailey et al. 2007) and similar (≈12 pps) to that observed for sternohyoid motor units in the present study. Thus intrinsic properties of motor neurons may vary across muscles, as may also be extrapolated from the analysis of results of animal studies. For example, Fung et al. (2000) reported an average duration of AHP at half-amplitude of ≈33 ms, with very limited spread among a population of hypoglossal motoneurons in the cat, whereas approximately half of the cat lumbar motor neurons investigated by Powers and Binder (2000) had AHP duration at half-amplitude ≥50 ms. Because genioglossus motor neurons are cranial, whereas sternohyoid motor neurons are spinal, the difference in minimum discharge rate with respect to limb muscles observed by Bailey et al. (2007) and in the present study is probably not related to the charac-

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**Fig. 4.** Example of sternohyoid motor unit behavior during a sustained contraction. A: one of the bipolar signals recorded during a sustained contraction. B: superimposed action potentials generated by the target motor unit, extracted from the recording on 4 channels of the array. C: instantaneous discharge rate of the target motor unit during the contraction. D: signal portions of 500 ms extracted from the recording, at the time intervals indicated by dashed lines in C.
teristics of the innervation but may be attributed to the fact that the genioglossus and sternohyoid are muscles with very specialized and complex functions with respect to limb muscles.

The most important difference of the present results with respect to those obtained from limb muscles is the high discharge rates achieved by the investigated motor units. Although very high, the observed discharge rates may not be the maximal that the investigated motor units could achieve because the subjects were asked to decrease the intensity of the contraction when the activity of other motor units was detected by the surface recording system. In fast bursts of activity, the instantaneous discharge rate peaked at about 170 pps (Fig. 6), which corresponds to a 5- to 6-ms interval between action potentials. This interval is close to the absolute refractory period for muscle fibers and probably within the relative refractory period (Kopec et al. 1978; Stålberg 1966). Instantaneous rates of about 90 pps were previously observed at the beginning of ballistic contractions of the tibialis anterior muscle (Van Cutsem et al. 1998); in the present study, similar or higher rates could be reached repetitively in the sternohyoid muscle with relatively short rest intervals between bursts (Fig. 6). Bailey et al. (2007) also observed very high rates (~80 pps) of genioglossus motor units, which were recruited sporadically for brief periods during slow protrusions and static holding tasks of the tongue. These high rates were not sustained during the task and could have represented the activity of motor units responsible for rapid tongue movements, sporadically recruited during the slow tasks analyzed by Bailey et al. (2007). In the present study, high rates were observed not only in brief bursts of activity but also during sustained activation.

Instantaneous discharge rates >100 pps were often observed during the sustained contractions (Figs. 4 and 5). The occurrence of high-frequency bursts of discharges during the sustained contractions was more pronounced than that observed in limb muscles (e.g., Christie and Kamen 2006). When an individual performs either a steady contraction or one in which the force increases gradually, motor units in some limb muscles discharge pairs of action potentials with an ISI <20 ms; this is often referred to as a double discharge or a doublet (Bawa and Calancie 1983; Christie and Kamen 2006; Garland and Griffin 1999). However, these discharges are rare, and the occurrence of more than two action potentials at a very short

**FIG. 5.** Discharge rate histograms during a sustained contraction. A: instantaneous discharge rate during a sustained contraction. The discharge rate averaged in overlapping intervals of 200 ms is shown in solid line. B: signal portions of 500 ms extracted from the recording, at the time intervals indicated by dashed lines in A. C–E: histograms of instantaneous discharge rates during the first 10 s (C), the middle 10 s (D), and the last 10 s (E) of the contraction. The dashed vertical lines indicate the mean value for discharge rate, also numerically reported.
distance is unlikely because of the period of hyperpolarization following a doublet (Calvin and Schwindt 1972), which would require large synaptic input to elicit another discharge. Bursts of three potentials at a distance <20 ms in limb muscles were indeed observed only during dynamic contractions when the synaptic input may present large and rapid variations (Garland et al. 1996; Van Cutsem et al. 1998) or in contractions of transplanted hands after long periods of denervation (Farina et al. 2008). On the contrary, in this study double discharges (<20-ms separation) accounted for >50% of the total number of discharges of sternohyoid motor units during contractions at sustained maximal rate. Long sequences of consecutive discharges at rates >50 pps were commonly observed. In the bottom traces of Figs. 4 and 5 there are examples of series of several action potentials with this property. The percentage of action potentials with high instantaneous rates was consistent with the number of ISIs <20 or 10 ms, as theoretically predicted by the observed mean value and variability of the ISI. Thus very short ISIs were not special cases but part of the normal activation pattern of these motor units. The variability of the ISI (~40%) was indeed very large compared with that observed in other muscles (Barry et al. 2007). For example, for the first dorsal interosseus muscle, the CV for the ISI was found to be about 25% at recruitment and decreased to about 14% with an increase in discharge rate in young adults (Barry et al. 2007). The ISI variability observed in the present study was also substantially greater than the variability reported for other orofacial muscles (Bailey et al. 2007). For example, genioglossus motor units have discharge variability of close to 20% during volitional tasks (Bailey et al. 2007) and a large proportion of motor units in intrinsic laryngeal muscles have variability <10% during phonation (Luschei et al. 1999). However, in the present study the motor units were activated in a different way with respect to previous studies (with a visual feedback on action potentials); thus direct comparison is not possible.

The discharges occurring at rates considered exceptionally high in limb muscles were common discharges in the muscle analyzed in the present study as a consequence of the high mean value and variability of the ISI. The cause of the large discharge rates observed may be related to exceptionally large synaptic input received by these motor neurons, perhaps in relation to the function of this muscle. The synaptic input to motor neurons is ionotropic and metabotropic (neuromodula-
The neuromodulatory input determines the motor neuron excitability, thus affecting the motor neuron intrinsic properties, and may provide a substantial contribution to the net current generating the repetitive discharge of action potentials (Heckman et al. 2008). The present results may be explained by high excitability of the motor neurons through activation of persistent inward currents (metabotropic input) in combination with high ionic and metabotropic inputs to be identified. The high discharge rates may serve to produce rapid movements required for the displacement of the hyoid bone and larynx during deglutition or phonation. Similarly, the high discharge rates observed for some genioglossus motor units may determine rapid tongue movements (Bailey et al. 2007).

The observed variability in interspike interval was very high. The variability in discharge rate is due to synaptic noise and its interaction with the time course of the postspike AHP of the motor neuron (Calvin and Stevens 1967; Matthews 1996; Stein et al. 2005). In addition to possible differences in AHP between the sternohyoid and limb muscles, a greater synaptic noise may be due to a larger synaptic input received by the motor neurons (Berg et al. 2007). An increase in synaptic input indeed requires the integration of excitatory and inhibitory inputs, which determines an increase in noise of the membrane voltage trajectory (Berg et al. 2007; Stein et al. 2005). However, large synaptic input seems to be insufficient in other muscles for high discharge rates to be reached because of rate saturation (Bailey et al. 2007; Johns and Fuglevand 2004); thus the higher rates observed in the sternohyoid muscle may also reflect differences in intrinsic motor neuron properties with respect to limb muscles.

In summary, motor neurons of the sternohyoid muscle can reach instantaneous discharge rates >150 pps and can maintain average rates of activation >60 pps during sustained contractions with visual feedback on motor unit action potentials. These rates and their variability are substantially higher than those previously observed in limb muscles.

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