Firing Patterns of Human Genioglossus Motor Units During Voluntary Tongue Movement

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INTRODUCTION

The tongue is a remarkable structure that participates in a range of complex oromotor behaviors including mastication, swallowing, breathing, and speaking. The muscles of the tongue differ from those of limbs in several important ways. They do not act on a lever or tendon and exhibit few spindles organs (Cooper 1953; Kubota et al. 1975), and there is scant evidence for either Renshaw-like recurrent inhibition or monosynaptic excitatory stretch reflexes (Cooper 1953; Porter 1966). Because the tongue lacks a bony skeleton, tongue muscles make nontendinous insertions into lingual soft tissue and overlap and interdigitate extensively and at various orientations throughout the tongue (Abd-El-Malek 1938). This interdigitation severely limits the EMG assessment of motor unit activities within the body of the tongue and continues to pose a considerable technical challenge to in vivo force measures traditionally used in limb or digit muscles.

In this study, we recorded single motor unit activities from a tongue protruder muscle, the genioglossus (GG), and asked the following questions: 1) are the firing rates of GG motor units (MUs) comparable with those observed in other orofacial or limb muscles, 2) is interspike interval variability of GG MUs comparable with that observed in other orofacial or limb muscles, and 3) are individual GG MUs recruited at the same position in space on successive volitional protrusions. Importantly, we show that both the recruitment and rate modulation of GG MUs seem precisely tuned to tongue position.

METHODS

We performed 14 experiments in 10 healthy human volunteers (5 women and 5 men; age, 22–48 yr). All experimental procedures were approved by the Human Subjects Committee at The University of Arizona. Subjects gave their informed consent before participation in the study.

EMG recording

Single motor unit action potentials were recorded with submental tungsten microelectrodes inserted transcutaneously into the GG (1- to 5-μm tip diameter, 250-μm shaft diameter, 10 MΩ at 1 KHz; Frederick Haer, Bowdoinham, ME). A surface electrode (4-mm-diameter Ag-AgCl) attached to the skin overlaying the mastoid process served as an indifferent electrode, and both the intramuscular and surface electrodes were referenced to a ground strap placed around the upper arm. Motor unit potentials were amplified (1,000×), band-pass filtered (0.3–3 KHz; Grass Instruments, West Warwick, RI), and displayed on a storage oscilloscope and recorded on the Spike2 data acquisition and analysis program (CED, Cambridge, UK).

Intramuscular electrode placements were made ~1.5 cm on either side of the midline at a distance ~2–4 cm from the inferior margin of the mandible. To define the minimum depth for electrode insertion, the musculature of the floor of mouth initially was visualized by ultrasonography (Pro Sound 3500, Aloka, Tokyo, Japan), and the distance from the skin surface to the inferior border of the GG muscle was determined using an electronic caliper (Eastwood et al. 2003). The average depth to the inferior border of the genioglossus muscle was 13–15 mm, and MU activities were typically recorded at depths 18–24 mm from the skin surface.

Protocol

Subjects were seated upright in a dental chair with their head supported. Respiratory movements of the chest were monitored by a respiratory effort transducer (Biopac Systems, Goleta, CA) positioned around the rib cage at the level of the axilla. Protrusion-retraction–related displacement of the tongue was detected by a battery powered isotonic transducer (Harvard Apparatus, Kent, UK). The transducer was connected to the tongue by a customized lever arm that engaged a thermoplastic housing (Fig. 1). The housing was affixed to the dorsum of the tongue in a two-step process. First, a foundation layer (polycarboxylate cement, ESPE America,
Norristown, PA) was applied to the the distal portion of the tongue, after the tongue had been dried with gauze. After the foundation material had dried, cyano-acrylate glue (Ellman International, Ocean-side, NY) was used to secure the housing to the foundation layer. At the termination of the experiment, the foundation layer could be readily removed from the tongue without causing discomfort to the subject. The coupling posed minimal impediment to movement, and subjects were able to swallow and speak during the experiment. The displacement signal was amplified (Grass) and displayed using the Spike2 data acquisition and analysis program (CED).

Tongue tip position (mm) was referenced to a neutral (or resting) position, in which the jaw was relaxed, the mouth slightly open, and the tongue-tip visible just behind the lower incisors. Positive position values indicated protrusion of the tongue beyond the neutral position, whereas negative values indicated retraction from this position.

Each trial comprised a static holding task and three slow protrusions. Subjects were provided with both auditory and visual feedback (i.e., through an ongoing display of the spike record on a slowed time scale) of the discharge in both the static hold and protrusion tasks. For the holding task, subjects were instructed to maintain the tongue in the least-protruded position that was also associated with stable MU discharge (i.e., firing without interruption) for 20 s.

For slow protrusions, subjects first retracted the tongue (i.e., relative to the position during the holding task) and slowly advanced the tongue to recruit the target motor unit. Slow protrusion continued until the activity of additional motor units were detected on the electrode, whereupon the subjects were instructed to slowly retract the tongue until discharge in the target motor unit ceased. Each protrusion/retraction lasted ~30 s and was repeated three times in quick succession. Trials in which swallows occurred between successive protrusions were excluded from the analysis.

Data analysis

Data were analyzed using Spike2 and custom-designed software. Initially, motor units were discriminated using a template-matching algorithm based on waveform shape and amplitude. For an analysis of firing rate during protrusions, only those units whose activity could be followed in three protrusions were included. Recruitment firing rate was calculated from the first 10 interspike intervals during the tongue protrusion task, and peak firing rate was determined as the highest rate for 10 consecutive interspike intervals during the task. Mean values for recruitment and peak firing rates were calculated from the three trials that were recorded for each motor unit. The average GG firing rate was calculated as the reciprocal of the average interspike interval (ISI) over the entire period of tonic discharge associated with the holding task. Variability in ISIs during the holding task was estimated as the coefficient of variation (CV) of the ISIs, expressed as a percentage [CV = (SD ISI/mean ISI) × 100].

RESULTS

We recorded a total of 50 single GG motor units. Figure 2 shows representative data for a single GG motor unit during four trials with increasing tongue displacement across trials. The unit was recruited at approximately the same tongue position on successive protrusions (0.14, 0.18, 0.13, and 0.51 mm). Firing rate initially increased steeply with tongue displacement beyond the recruitment position, from an initial mean rate in this unit of 12 ± 2 (SD) Hz up to a mean peak rate of 13.6 ± 2 Hz. However, for tongue displacements 4–6 mm beyond the recruitment position, there was little additional modulation in firing rate. This leveling-off in firing rate is highlighted when contrasting the overall extent of tongue displacement across the four trials—from 6.4 mm in the first trial to 13.6 mm in the fourth trial—yet the peak rates are nearly the same across trials (Fig. 2, horizontal dashed line). Furthermore, for trials 2–4, other units were recruited at times when the discriminated unit had ceased to increase its firing rate, implying that the overall neural drive to the GG motoneuron pool continued to increase throughout tongue protrusion.

Figure 3 shows the relationship between firing rate and tongue displacement for all 50 units. Each trace represents a third-order polynomial fit to the firing rate–displacement curve.
for each unit. The maximal displacement shown in each trace simply represents the tongue position at which the activity of the target unit began to be obscured by activity of other units. Consequently, the highest firing rate shown for each unit in Fig. 3 should not necessarily be taken to represent the maximal firing rate of the unit. Nevertheless, for most of the GG units recorded, firing rates seemed to level off at displacements less than that at which discrimination became unreliable. The majority of units (44/50) exhibited considerable displacement associated increases in firing rate (i.e., >10 Hz). The other six units (all from 1 subject), however, exhibited only modest increases in firing rate (<5 Hz). Overall, the average peak firing rate for all units was 24.6 ± 6.2 Hz.

In comparison, the average firing rate during the holding task was 16.1 ± 4.2 Hz. This firing rate was somewhat higher than that measured at the outset of the tongue protrusion task (13.1 ± 3.3 Hz), presumably because of the requirement to maintain secure tonic discharge for the full period of the hold. We also used the holding task to examine the variability of the ISIs. The CV of the ISIs measured was 20.6%, comparable with that found in most limb motor units (Clamann 1969; Macefield et al. 2000; Nordstrom et al. 1992).

On occasion, we encountered motor units that exhibited transient responses with remarkably high instantaneous firing rates up to ~80 Hz. Whereas these units appeared to discharge sporadically or not at all during the slow tongue protrusions or the static holding task, they appeared to be robustly activated during rapid movements.

**DISCUSSION**

This study provides the first data on the firing patterns of human lingual motor units during a voluntary task. We characterized the relation between firing rate and displacement during tongue protrusions. For most GG motor units, firing rate increased steeply with tongue protrusion over a relatively limited displacement range, beyond which firing rate appeared to saturate. Such saturation in firing rate has been described previously for limb motor units (Johns and Fuglevand 2004; Monster and Chan 1977). While several possible causes of firing rate saturation have been discussed in the literature (Destexhe and Pare 1999; Heckman and Binder 1993; Taylor and Enoka 2004), the actual mechanisms underlying firing rate saturation have not yet been clearly delineated. Nevertheless, we showed that firing rate saturation is a prominent feature of hypoglossal motoneurons.

The average rate at which GG MUs were found to discharge tonically during the holding task was substantially higher than that reported for most limb motor units, which typically discharge at ~6–10 Hz under similar conditions (Andreassen and Rosenfalck 1980; Hockensmith et al. 2005; Monster and Chan 1977). Because minimum firing rate is known to be inversely related to the duration of the afterhyperpolarization (AHP) after the action potential (Kernell 1965), perhaps human hypoglossal motoneurons possess briefer AHPs than do spinal motoneurons, as seems to be the case in the cat (Fung et al. 2000; Powers and Binder 2000).

Remarkably, GG MU recruitment seemed to be precisely related to a specific tongue position. For example, activity of the unit depicted in Fig. 2 reliably started within 0.5 mm of the same tongue position across four independent protrusions. Overall, recruitment of GG MUs was seen to occur throughout a wide range of tongue positions, with some units recruited at tongue positions less than the relaxed or “neutral” position (Fig. 3). Thus there is likely some degree of tonic motor unit activity in the GG even during presumed resting conditions.

Last, we encountered some motor units whose activity patterns were difficult to characterize within the parameters of our slow protrusion task. These units discharged transiently and at high firing rates during rapid tongue movements. Based on these preliminary observations, it seems possible that the GG motoneu-
The cause of this apparent task-related difference in discharge
related GG MUs is also very low (H11011/charge variability in both inspiratory and tonic respiratory-CVs of H11021 to E. F. Bailey and NS-39489 to A. J. Fuglevand.

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**REFERENCES**


