Sleep/Wake Firing Patterns of Human Genioglossus Motor Units

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INTRODUCTION

Research in the area of obstructive sleep apnea (OSA) has long focused on the upper airway and in particular on the consequences of the loss of the “wakefulness” input on the whole muscle electromyographic (EMG) activities of the pharyngeal dilator muscle, genioglossus (GG). Such studies demonstrate that in wakefulness the GG muscle has a clear inspiratory phasic (i.e., greater activity in inspiration) pattern of activity superimposed on a background of tonic (i.e., present throughout the respiratory cycle) activity. Importantly, sleep does not appear to differentially affect either component of whole muscle GG EMG, consistent with the view that both phasic and tonic GG activities contribute to preserved airway patency (Tangel et al. 1992).

That the motoneuronal activities constituting whole muscle GG EMG are more complex than suggested by the phasic/tonic dichotomy is evident from the results of a recent study of hypoglossal motor unit (MU) activities in wakefulness (Saboisky et al. 2006). Beyond the traditional categories of phasic and tonic activities the authors characterized six principal MU types based on firing pattern and the relation to the respiratory cycle. Many of these MUs (~44%) exhibited inspiratory phasic activities, but slightly more than half the MUs recorded were classified as “tonic.” Interestingly, the majority of these tonic MUs also exhibited either inspiratory- and, in rare cases, expiratory-related increases in firing frequency, indicative of respiratory modulation.

To date, no comparable study has characterized single GG MU activities both in wakefulness and in sleep. Thus it is unclear whether the range of discharge patterns evident in wakefulness is preserved in sleep or whether certain “types” of MU are more or less susceptible to the removal of the wakefulness input. Accordingly, we sought to characterize GG MU activities separately for wakefulness and NREM sleep based on the relationship between the firing pattern and the respiratory cycle (Netick and Orem 1981; Orem and Dick 1983). In view of evidence of sleep-associated increases in whole muscle GG EMG activities in healthy human subjects two to three breaths after the wake–sleep transition (Tangel et al. 1992; Worsnop et al. 1998, 2000), we anticipated that inspiratory phasic and background tonic motor unit activities would be robustly preserved in NREM sleep.

Second, in view of the recent work of Saboisky et al. (2006) that documents respiratory modulation of tonic GG MU activities in wakefulness, we sought to quantify the magnitude of the modulation and to ascertain the effect of NREM sleep on this aspect of MU activities. Earlier work by Orem and colleagues assessed the correlation between the activities of central respiratory neurons and the ventilatory cycle and quantified the strength of that association using the eta ($\eta^2$) index (Orem and Dick 1983). In this study, we adapted this technique, using it to assess the relative strength of the respiratory modulation of single GG MU activities in wakefulness and subsequently in NREM sleep. This enabled us to test a second hypothesis that the strength of respiratory modulation is a stable characteristic of single GG MU activities.

METHODS

We performed 25 experiments in 17 healthy human volunteers (10 women and 7 men, ages 22–55 yr (averages: age: 30±8.8 yr; height: 168±4.1 cm; weight: 67±12.1 kg; body mass index: 23.3±2.4). All subjects were in good health, free of skeletal abnormality, without history of major surgery or injury involving the respiratory system, without neural or respiratory disease or disorder, without history of sleep disorders, and free of any medication that could affect nervous system function. The Human Subjects Committee at The University of
Arizona approved all experimental procedures. Subjects gave their informed consent before participation in the study.

**Electromyographic (EMG) recordings**

Single motor unit action potentials (SMUAPs) recorded from GG were obtained using tungsten microelectrodes (1- to 5-μm tip diameter, 250-μm shaft diameter, 10 MΩ at 1 kHz; FHC, Bowdoinham, ME). A surface electrode (4-mm diameter Ag–AgCl) attached to the skin overlying the mastoid process served as an indifferent electrode, and both 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 to monitor the size and shape of the MU impulses and recorded on the Spike2 data acquisition and analysis program [Cambridge Electronic Design (CED), Cambridge, UK]. Whole muscle GG EMG activities were obtained in the same manner but for these recordings the terminal 10 mm of the microelectrode tip was bared of insulation. SMUAPs were recorded both ipsilateral and contralateral to recordings of EMG from the whole muscle.

To optimize electrode placement, the musculature of the mouth floor was initially visualized by ultrasonography (Pro Sound 3500; Aloka, Tokyo, Japan) and the distance from the submental surface to the inferior border of the GG muscle was determined using an electronic caliper (Eastwood et al. 2003). To preserve motor unit recordings in quiet wakefulness and during sleep necessitated a specialized arrangement of the experimental setup as follows. First, although tungsten microelectrodes render recordings of remarkable fidelity and permit in situ manipulation of the electrode, their use places considerable constraints on subject position and movement. Thus all the experiments in this study were conducted with subjects in the supine position in a dental chair. Second, to preserve electrode position across wakefulness and sleep, we inserted electrodes more posteriorly and to depths >20 mm. These coordinates typically rendered the most productive and stable MU recording sites relative to more superficial and/or anterior locations (see Fig. 1).

Respiratory movements of the chest were monitored by a respiratory effort transducer (Biopac Systems, Goleta, CA) positioned at the midsternal level and at the level of the umbilicus. Output from these sensors reflected changes in the anteroposterior dimensions of the rib cage and abdomen. These signals were used to estimate thoracic expansion and to define the inspiratory and expiratory portions of the respiratory cycle.

**Polysomnographic recordings**

Electrodes were placed according to the international 10–20 system using a referential montage with central (C3/A1) and occipital (O1/A2) electroencephalogram (EEG) derivations, and right and left outer canthus to obtain electrooculogram (EOG) recordings. Signals were amplified (sensitivity 7.0 μV mm⁻¹), band-pass filtered (0.3–100 Hz; Grass Instruments), and relayed to the Spike2 data acquisition unit.

**Protocol**

Subjects were instructed to refrain from consuming any caffeinated products in the 12 h leading up to the study. To facilitate subjects’ sleeping during the experiment, subjects were asked to retire about 2 h later than the usual bed time the night before. All experiments were conducted in the early afternoon, commencing around 1:30 pm. Subjects lay supine, head supported, in a dental chair. Each trial consisted of periods of quiet wakefulness and NREM sleep. Subjects were provided with a manual clicker and instructed to rest quietly with their eyes closed and to depress the clicker until instructed otherwise. This enabled subjects to maintain quiet wakefulness and obviated the need for verbal communication that might otherwise displace the needle electrode. After 2–3 min of stable wakefulness, the “clicker” was removed from the subject’s hand and the subject was instructed to rest quietly with eyes closed and the subject was allowed to fall asleep. After recording in quiet wakefulness and sleep, the subject was awakened and another MU was sought. If a MU with significantly different firing pattern and shape (as seen on the oscilloscope) was found it was considered to be a distinct MU and the protocol was repeated. Lights remained off throughout the recording period and subjects were exposed to a broadband noise (~85 dBA) that masked their own breath sounds and external noise sources. Subjects were not required to perform any maneuvers that might activate GG motor units nor were they provided with visual or auditory feedback of respiratory-related movements or motor unit activities.

**Data analysis**

All data were acquired using Spike2 software (CED). Subsequent off-line analysis of EMG activities was performed using customized computer software (Spike2).

**Sleep scoring.** Periods of sustained wakefulness and uninterrupted sleep were identified using the following criteria. For each subject, EEG activity initially was assessed as being predominantly alpha (8–12 Hz) or theta (4–7.75 Hz) wave activity on the basis of sequential 30-s epochs using the criteria of Rechtschaffen and Kales (1968). Sleep onset was defined as two consecutive epochs of Stage 1 or one epoch of Stage 2, free from overt EEG arousals (>3.0 s) (ASDA 1992; Loredo et al. 1999). Awakening was defined as an instance of >1 min of wakefulness occurring after sleep onset. In addition, power spectral analyses were performed on the C3/A1 derivation on six consecutive 5-s epochs using commercial software (Spike2, CED). In this manner, multiple nonoverlapping windows were averaged to yield 30-s epoch (0.5-Hz resolution). Power spectral distributions were computed for the following bandwidths: slow-wave activity (0.75–4.5 Hz), theta (4.0–7.75 Hz), alpha (8.0–12.0 Hz), sigma (12.25–15.0 Hz), and beta (15.25–31.0 Hz) for 10–15 consecutive breaths in wakefulness and 10–15 consecutive breaths in NREM sleep.
MOTOR UNIT DISCRIMINATION. Motor units were discriminated using a template-matching algorithm based on waveform shape and amplitude. Subsequently, each waveform was checked by visual inspection against the template unit waveform. Only those units that were active in quiet wakefulness and persisted in NREM sleep or were reactivated on awakening from sleep were included in the analysis.

Initially, we characterized motor unit discharge pattern on the basis of the temporal relationship between the spike train and the respiration cycle based on the summed ribcage and abdomen volume excursions. Briefly, we used a zero and peak crossing algorithm to divide each breath into an inspiratory portion and expiratory portion and then each of these partitions into two equal parts corresponding to early and late inspiration (P1 and P2) and early and late expiration (P3 and P4). Motor units were considered tonic if their activities persisted throughout each of the four phases of the respiratory cycle for 10–15 consecutive breath cycles. Conversely, motor units were considered phasic if discharge ceased in one or more of the phases of the respiratory cycle for 10–15 consecutive breaths. The categorization of MUs on the basis of discharge pattern was conducted separately for wakefulness and NREM sleep.

We assessed the strength of the relationship between MU activities and the respiratory cycle by one-way ANOVA (Netick and Orem 1981) and quantified the magnitude of the association between a motor unit’s activities and the respiratory cycle using the eta (\(\eta^2\)) value (Netick and Orem 1981; Orem and Dick 1983; Orem et al. 2002). In this study, the \(\eta^2\) value indicates the proportion of the total variance (SS\text{total}) of a MU’s activities over a series of breaths that is made up by variance between phases of the respiratory cycle and is calculated as follows: \(\eta^2 = \frac{SS\text{between}}{SS\text{between} + SS\text{within}}\), where SS\text{between} represents the variability between groups (i.e., the range in impulse/count means across the four phases of a respiratory cycle) and SS\text{within} represents the variance within groups (i.e., the variability in impulse/count across 10–15 breaths within individual phases of the respiratory cycle). Using this approach we calculated \(\eta^2\) for individual motor units based on 10–15 breaths in quiet wakefulness and 10–15 in uninterrupted NREM sleep. We subsequently averaged eta values obtained from individual MUs to derive an eta value for the group in wakefulness and sleep. Paired t-tests were used to determine statistical significance of the change in \(\eta^2\) values separately between wakefulness and NREM sleep. Statistical significance was set at \(P < 0.05\).

RESULTS

Single motor unit (SMU) recordings were obtained at locations about 1.0–1.5 cm on either side of the midline and at a distance about 2.0–3.5 cm from the inferior margin of the mandible (Fig. 1). The average depth to the inferior border of the GG muscle was 12–14 mm and SMU activities were typically recorded at depths 22–28 mm from the skin surface at electrode angles of about 45\(^\circ\) to the horizontal (see Fig. 1, location B).

We recorded the activities of 81 GG motor units. The number of motor units studied per subject ranged from 3 to 7. Our analysis revealed consistently low ISI variability (\(6–11.0\%\)) but considerable heterogeneity in average discharge frequency (range 8.0–28.3 Hz). We were successful in recording 64 single GG MUs in quiet wakefulness and in NREM sleep. An additional 17 motor units that were inactivated at sleep onset, but recruited on awakening, were also recorded. Many other motor units were detected in quiet wakefulness but fell silent in NREM sleep and were not recruited on awakening. The latter MUs are not included in the present analysis. In all cases in NREM sleep, the peak power fell in the \(\theta\) (4.0–7.75 Hz) or slow-wave (0.75–4.0 Hz) bandwidths.

Figure 2 depicts frequency histograms of all GG MUs as a function of the eta (\(\eta^2\)) value, in wakefulness and NREM sleep. In wakefulness, the distribution is bimodal with the majority (\(n = 55\)) of MUs exhibiting moderate to weak respiratory-related modulation (\(\eta^2 <0.60\)). The remaining MUs exhibited strong respiratory modulation (\(\eta^2 >0.6\)). Whereas the total number of active MUs declined (\(n = 64\)) in NREM sleep, there was no significant difference in the magnitude of respiratory modulation of the population of MUs in wakefulness versus
of the corresponding discharge in wakefulness and in NREM sleep and on the basis of the pattern of respiratory modulation was lost.

These MUs typically discharged tonically, i.e., throughout inspiration and expiration in quiet wakefulness with moderate respiratory modulation (\(\eta^2 = 0.3-0.6\)). In NREM sleep, the tonic discharge pattern persisted but the magnitude of the respiratory modulation was diminished (\(\eta^2 < 0.30\)) relative to quiet wakefulness.

A second group of MUs discharged phasically in wakefulness and converted to tonic discharge in NREM sleep (\(n = 10\)). These MUs, designated phasic–tonic, were strongly modulated (\(\eta^2 > 0.6\)) in wakefulness (see Fig. 4) attaining peak discharge in early inspiration and falling silent during expiration. In NREM sleep, the strength of the respiratory modulation declined (\(\eta^2 = 0.3-0.6\)) and the discharge pattern changed such that activities persisted through all phases of the respiratory cycle.

Representative recordings of the third MU pattern (\(n = 13\)), designated tonic–phasic, are depicted in Fig. 5. These MUs discharged tonically in wakefulness converting to a phasic discharge pattern in NREM sleep. The majority of these MUs (\(n = 9\)) exhibited moderate to weak respiratory modulation in wakefulness (\(\eta^2 < 0.6\)) that increased in NREM sleep (\(\eta^2 > 0.60\)). However, a smaller subset (\(n = 4\)) appeared distinct from all other MUs in that tonic discharge in wakefulness converted to episodic bursting activity in NREM sleep (see Fig. 6) with negligible respiratory modulation (\(\eta^2 < 0.3\)).

Figure 7 shows corresponding impulse histograms for the MUs depicted in Figs. 3–5. Each histogram depicts the impulse count/bin (0.2 s) for inspiratory (I) and expiratory (E) portions of two breath cycles in wakefulness and in NREM sleep and the associated \(\eta^2\) value for that motor unit. The topmost histograms (Fig. 7A) are representative of motor units with tonic–tonic discharge patterns with weak respiratory modulation (\(\eta^2 < 0.3\)) in wakefulness and sleep. By comparison, phasic–tonic MU types (Fig. 7B) were characterized by strongly respiratory modulation in wakefulness (\(\eta^2 > 0.6\)) but exhibited weak to moderate respiratory modulation in NREM sleep (\(\eta^2 = 0.3-0.6\)) (\(P < 0.05\)). In contrast, motor units with tonic–phasic discharge patterns (Fig. 7C) exhibited the reverse pattern of activity, i.e., moderate respiratory modulation (\(\eta^2 = 0.3-0.5\)) in quiet wakefulness that converted to strong respiratory-related modulation (\(\eta^2 > 0.6\)) in NREM sleep (\(P < 0.05\)).

The effects of sleep on discharge frequency also varied. Figure 8 depicts group average discharge frequencies for the

TABLE 1. Categorization of motor unit activities based on traditional classification scheme

<table>
<thead>
<tr>
<th>Discharge Pattern</th>
<th>Wakefulness (\eta^2)</th>
<th>NREM Sleep (\eta^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tonic (\rightarrow) tonic</td>
<td>Weak 13</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Moderate 25</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Strong 0</td>
<td>0</td>
</tr>
<tr>
<td>Phasic (\rightarrow) tonic</td>
<td>Weak 0</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Moderate 0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Strong 10</td>
<td>0</td>
</tr>
<tr>
<td>Tonic (\rightarrow) phasic</td>
<td>Weak 4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Moderate 9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Strong 0</td>
<td>9</td>
</tr>
<tr>
<td>Phasic (\rightarrow) phasic</td>
<td>Weak 0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Moderate 0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Strong 3</td>
<td>3</td>
</tr>
<tr>
<td>Tonic (\rightarrow) extinction</td>
<td>Weak 3</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Moderate 0</td>
<td>0</td>
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<td></td>
<td>Strong 0</td>
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<tr>
<td>Phasic (\rightarrow) extinction</td>
<td>Weak 0</td>
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<td></td>
<td>Moderate 0</td>
<td>0</td>
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<tr>
<td></td>
<td>Strong 14</td>
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</tbody>
</table>

Leftmost column shows motor units (MUs) grouped in accordance with traditional classification scheme; i.e., phasic or tonic based on discharge pattern evident in wakefulness and in stable NREM sleep. Rightmost columns show the corresponding number of MUs in each eta category: weak (\(\eta^2 < 0.3\)), moderate (\(\eta^2 = 0.3-0.6\)), and strong (\(\eta^2 > 0.6\)) respiratory modulation in wakefulness and in NREM sleep, although the clear bimodality of the distribution was lost.

We subsequently categorized MU activities using traditional designations, i.e., tonic or phasic based on the pattern of discharge in wakefulness and in NREM sleep and on the basis of the corresponding \(\eta^2\) category: weak, moderate, or strong in each state (see Table 1). There was no significant effect of state on MU type (\(P < 0.258\)).

Representative raw recordings of the prevailing MU types are shown in Figs. 3–6. Of the total number of MUs recorded in wakefulness and NREM sleep (\(n = 64\), the majority (\(n = 38\)) exhibited activities comparable to those depicted in Fig. 3. These MUs typically discharged tonically, i.e., throughout inspiration and expiration in quiet wakefulness with moderate respiratory-related modulation (\(\eta^2 = 0.3-0.5\)). In NREM sleep, the tonic discharge pattern persisted but the magnitude of the respiratory modulation was diminished (\(\eta^2 < 0.30\)) relative to quiet wakefulness.

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The effects of sleep on discharge frequency also varied. Figure 8 depicts group average discharge frequencies for the
principal MU categories in each of the four phases of the breath cycle in wakefulness (left) and NREM sleep (right). Consistent with the raw recordings, tonic–tonic MUs showed no significant state-related change in average discharge frequency (average 19.8–22.5 Hz), although the absolute distribution of discharge frequencies broadened in NREM sleep. In contrast, phasic–tonic and tonic–phasic MUs exhibited significant alterations in discharge frequency as a function of state. Phasic–tonic MUs attained peak frequencies (∼19.6 Hz) in early (i.e., Phase 1) and, in some cases, late inspiration (i.e., Phase 2) that declined to zero in late expiration. In NREM sleep, discharge persisted throughout the respiratory cycle with comparable discharge frequencies (∼17.3–20.5 Hz) in each of the four phases of the respiratory cycle. The tonic–phasic MUs exhibited the reverse pattern, discharging at slightly higher average frequencies (∼22.5–28.4 Hz) throughout the respiratory cycle in wakefulness and converting to inspiratory-only bursts in NREM sleep. Despite a sleep-associated decline in average discharge frequency, this decline failed to attain significance (P < 0.07). Thus when considered as a population, the absolute discharge frequency was preserved within a given phase of the breath across wakefulness and sleep states.

**DISCUSSION**

Although studies of the whole muscle GG EMG indicate that GG activities are preserved in NREM sleep, to date it has been unclear what influence sleep exerts on individual motor unit activities. The present recordings confirm a rich pattern of tongue muscle activation in wakefulness attributable to considerable heterogeneity in discharge rate and timing of GG MU discharge with respect to phases of the respiratory cycle. The tonic–phasic MUs exhibited the reverse pattern, discharging at slightly higher average frequencies (∼22.5–28.4 Hz) throughout the respiratory cycle in wakefulness and converting to inspiratory-only bursts in NREM sleep. Despite a sleep-associated decline in average discharge frequency, this decline failed to attain significance (P < 0.07). Thus when considered as a population, the absolute discharge frequency was preserved within a given phase of the breath across wakefulness and sleep states.
with weak to moderate respiratory modulation persist and, in some cases, the magnitude of the respiratory modulation of these MUs increased. Accordingly, we report robust GG MU activities in NREM sleep with a slight but nonsignificant increase in the overall strength of the respiratory-related modulation (see Fig. 2).

Critique of method
To determine whether the strength of respiratory modulation of motor unit activities varies as a function of state we adapted the method previously used by Orem and Dick (1983) to characterize the proportion of a cell’s activity that is attributable to a respiratory component. There are two important distinctions between the approach outlined by Orem and Dick (1983) and the current protocol. First, in the original method the $\eta^2$ value was determined on the basis of 50 breath cycles, with each breath cycle divided into 20 equal parts (Orem and Dick 1983). In the present study, statistical analysis of the data was completed on a smaller numbers of breaths (10–15 breaths) and with fewer divisions per breath cycle (4 parts). Whereas this technique allowed us to consider activities in terms of early inspiratory or expiratory, the approach rendered significantly higher values of $\eta^2$ than those reported in dorsal and ventral respiratory groups (Orem and Dick 1983).

Respiratory modulation of MU discharge
The focus in the current study was the relative stability of the $\eta^2$ value across wakefulness and NREM sleep. We found that about 30% of GG MUs changed discharge pattern with sleep and for the majority of these MUs the $\eta^2$ value also changed. Thus, whereas the absolute magnitude of respiratory modulation of the population of MUs did not change significantly from wakefulness to sleep ($\eta^2 = 0.38$ vs. 0.40), the effects of sleep on individual MU activities varied considerably with about 16% of MUs exhibiting significant decreases in respiratory modulation and about 14% exhibiting significant increases in the strength of respiratory modulation. Thus, the strength of respiratory modulation, although not a stable feature of individual GG motor unit activities, may be a stable feature of the population.

Motor unit discharge pattern
WAKEFULNESS. Only one other study has systematically quantified GG single MU activities in awake human subjects (Sab-
and NREM sleep. MU types in each of the 4 phases of the breath cycle (P1–P4) in wakefulness. For the majority of MUs (Sauerland and Harper 1976).

Differences in recording site (see Fig. 1) (Sauerland and Harper 1976; Skatrud and Dempsey 1985; Rowley et al. 2001), airway resistance (Orem et al. 1977; Eastwood PR, Allison GT, Shepherd KL, Szollosi I, Hillman DR. American Sleep Disorders Association (ASDA) Atlas Task Force. EEG activities under comparable conditions (Fogel et al. 1994; Wheatley et al. 1993) it seems likely that the changes in MU activities reported here occurred in response to perturbations in the chemical and/or mechanical environment that were not controlled under the current protocol. Additional studies of this type designed to assess the effects of blood gases (Phillipson 1978), cardiopulmonary variables such as lung volume (Morrell et al. 2000; Rowley et al. 2001), airway resistance (Orem et al. 1977; Sauerland and Harper 1976; Skatrud and Dempsey 1985; Worsnop et al. 2000), and the effects of aging and/or obesity on GG MU activities, are therefore of critical importance and interest.

**Physiologic implications**

Despite a large proportion (~30%) of MUs that exhibited significant state-related changes in respiratory modulation and discharge frequency, these effects were not significant when the results were considered for the population of MUs as a whole. Thus GG MUs cannot be considered exclusively tonic background or phasic-respiratory; rather, the discharge pattern appears to be an inherently flexible feature of GG activities in healthy young adults.

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**REFERENCES**


**FIG. 8.** Individual and average (10–15 breath cycles) discharge frequencies for tonic–tonic (n = 38), phasic–tonic (n = 10), and tonic–phasic (n = 9/13) MU types in each of the 4 phases of the breath cycle (P1–P4) in wakefulness and NREM sleep.

For the majority of MUs (n = 41/64), the discharge pattern evident in wakefulness was conserved in NREM sleep. Of this majority, some 90% of the MUs (n = 38/41) discharged throughout the breath exhibiting subtle sleep-associated increases/decreases in discharge frequency suggestive of dynamic modulation. We were surprised to find that the diverse range of discharge patterns evident in wakefulness was preserved in NREM sleep. Indeed, in a few subjects, new discharge patterns emerged (see Fig. 6). Although the breadth of discharge patterns was preserved, many MUs (n = 23/64) switched discharge pattern with sleep; i.e., MUs with a phasic discharge pattern in wakefulness switched to a tonic pattern in sleep or vice versa. Thus GG MUs cannot be considered exclusively tonic background or phasic-respiratory; rather, the discharge pattern appears to be an inherently flexible feature of GG activities in healthy young adults.

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