Discharge frequencies of single motor units in human diaphragm and parasternal muscles in lying and standing

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Butler, J. E., D. K. McKenzie, and S. C. Gandevia. Discharge frequencies of single motor units in human diaphragm and parasternal muscles in lying and standing. J Appl Physiol 90: 147–154, 2001.—Single motor unit discharge was measured directly in diaphragm and parasternal intercostal muscles to determine whether neural drive to human inspiratory muscles changes between lying and standing. The final discharge frequency of diaphragmatic motor units increased slightly, by 1 Hz (12%; \( P < 0.01 \)) when subjects were standing [182 units, median 9.1 Hz (interquartile range 7.6–11.3 Hz)] compared with lying supine [159 units, 8.1 Hz (6.6–10.3 Hz)]. However, this increase with standing occurred in only two of six subjects, in one of whom tidal volume increased significantly during standing. Parasternal intercostal motor unit final discharge frequencies did not differ between standing [116 units, 8.0 Hz (6.6–9.6 Hz)] and lying [124 units, 8.4 Hz (7.0–10.3 Hz)]. The discharge frequencies at the onset of inspiration did not differ between lying and standing for either muscle. A larger proportion of motor units in both inspiratory muscles had postinspiratory frequencies at the onset of inspiration did not differ between standing [124 units, 8.4 Hz (7.0–10.3 Hz)] compared with lying supine [159 units, 8.1 Hz (6.6–10.3 Hz)]. However, this increase with standing occurred in only two of six subjects, in one of whom tidal volume increased significantly during standing. Parasternal intercostal motor unit final discharge frequencies did not differ between standing [116 units, 8.0 Hz (6.6–9.6 Hz)] and lying [124 units, 8.4 Hz (7.0–10.3 Hz)]. The discharge frequencies at the onset of inspiration did not differ between lying and standing for either muscle. A larger proportion of motor units in both inspiratory muscles had postinspiratory or tonic expiratory activity for lying compared with standing (15 vs. 4%; \( P < 0.05 \)). We conclude that there is no major difference in the phasic inspiratory drive to the diaphragm with the change in posture.

When a person changes posture from sitting to lying, functional residual capacity (FRC) decreases by \(-20\%\) (14). This means that the diaphragm is shorter in the standing posture than when lying supine (48, 49). Early studies of neural drive to the human diaphragm often used measurements of integrated surface electromyographic (EMG) activity recorded with a gastroesophageal catheter. With this method, it was found that phasic diaphragmatic EMG increased on average four- to fivefold when subjects changed posture from lying to standing (20). This has been interpreted to mean that neural drive must increase markedly to compensate for changes in “load” applied to the human diaphragm in different postures, perhaps through proprioceptive reflexes (20, 21, 28, 35, 36). These studies relied on the assumption that the EMG recording conditions for the crural diaphragm do not change with posture and that the EMG reliably reflects the efferent activity in the phrenic nerve. Previous workers had considered the possibility of artifactual changes in recording conditions but had regarded the effect as too small to have influenced the EMG results (27). However, during phrenic nerve stimulation, there are consistent artifactual changes in the amplitude of the maximal compound muscle action potentials with changes in lung volume and configuration of the rib cage and abdomen (24). The magnitude of this artifact appeared sufficient to conclude that the increased EMG when standing is probably explained by movement of the recording electrodes relative to the active muscle, at least for the crural diaphragm (24). Even with use of a multielectrode esophageal catheter, the artifacts are difficult to eliminate (16). Therefore, definitive measurement of neural drive requires a method unaffected by recording artifacts.

The discharge frequency of a motoneuron under normal conditions indicates the level of injected current or neural “drive” that it is receiving (30, 31). Thus, as neural drive increases, discharge rate increases. To assess the neural drive to human limb muscles, selective monopolar electrodes have been used to sample the discharge frequencies of single motor units during isometric contractions (e.g., Ref. 4). More recently, this technique has been adapted to derive motor unit discharge frequencies from human respiratory muscles during shortening and hence to measure neural drive without the limitations of surface electromyography (9, 18).

In the present study, we used recordings of single motor units to assess neural drive to the costal diaphragm and parasternal intercostal muscles during standing and lying. Any differences in inspiratory discharge rates of the diaphragmatic and the parasternal intercostal motor units were small and inconsistent.

METHODS

Experiments were performed in six healthy subjects (5 men, 1 woman) when they were standing upright or lying supine on a bed. Three subjects were aware of the purpose of the investigations, but this was considered unlikely to influence the results.

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Experimental setup. Recordings of single motor units were made using Teflon-coated monopolar electrodes with an exposed tip of 0.15 mm². The electrode was inserted through the right seventh or eighth intercostal space in the midclavicular line into the diaphragm in six subjects (5) and, on a separate occasion, through the right second or third intercostal space, 2 cm from the sternum, into the parasternal intercostal muscle in five of the six subjects (23). Precise location and depth of insertion of electrodes were guided by prior ultrasonography of the diaphragm and the chest wall (model XP128, Acuson, Mountain View, CA) in the two postures. For the diaphragm, the electrode was close to the origin of the costal fibers and below the reflection of the visceral pleura. One subject with a history of vasovagal syncope was premedicated with atropine (0.6 mg) injected intramuscularly. The reference surface electrodes were placed 2–3 cm from the monopolar electrode either over an adjacent rib for the diaphragm recordings or over the sternum for the parasternal intercostal muscle recordings. The electrode was determined to be recording the EMG activity from the muscle of interest and not from the adjacent muscles by using auditory feedback of muscle activity. In both experiments, the muscles of interest show increased activity during inspiration, while the adjacent muscles are expiratory in function.

Recording and analysis of data from single motor units. In each subject and posture (standing and lying supine), single motor unit activity was recorded from 10 sites within the diaphragm and parasternal intercostal muscles while the subjects were breathing quietly. All signals were sampled at 10 kHz (bandwidth 16–3,200 Hz; amplification ×5,000–10,000) and stored on both magnetic tape and disk for subsequent analysis (Spike 2, Cambridge Electronic Design, Cambridge, UK). At each recording site, usually two to four single motor units (range 1–5) could be distinguished on the basis of their size and shape by using custom-designed software (Fig. 1C; see also Ref. 23).

Plots of instantaneous frequency were derived. They allowed the measurement of the initial and final discharge frequency for each motor unit during each breath (Fig. 1D). The initial discharge frequency was calculated from the first interspike interval. Units that had a tonic or background discharge were not included in the analysis of initial discharge frequency. Units were defined as “tonic” if they discharged throughout respiration and had “postinspiratory activity” if they continued to discharge for >1 s after cessation of inspiratory expansion of the rib cage and abdomen.

The initial discharge frequencies were also compared for units recruited before and after the onset of inspiratory flow (defined by the onset of rib cage and abdominal expansion) during standing and lying. The initial (onset) discharge frequency of a diaphragmatic motor unit increases when inspiratory flow increases, irrespective of inspiratory duration (9). The final discharge frequency was calculated as the mean of the instantaneous discharge frequency of each motor unit between two cursors positioned manually around the last half of each inspiration when discharge rates had usually reached a plateau. For each unit, the initial discharge frequency and final discharge frequency were averaged over three consecutive breaths during quiet breathing.

Other respiratory measurements. Measurements of respiratory movements of the rib cage and the abdomen were made using calibrated inductance plethysmographs placed around the chest and the abdomen (Respitrace, Ambulatory Monitoring, Ardsley, NY). The gains of the signals were adjusted using the isovolume maneuver (11). End-tidal levels of CO₂ were monitored throughout by using an infrared analyzer (Ametek, Pittsburgh, PA). Subjects were instructed to breathe quietly for the duration of each experiment.

The inspiratory time (Ti), breathing frequency (f), and tidal volume (VT) were measured from respiratory movements and averaged over the three breaths for which motor unit activity was analyzed. Mean inspiratory flow (Vt/Ti), an estimate of inspiratory drive (13), and average minute ventilation (VE = VT × f) were calculated.

The relative contributions of movement of the rib cage and abdomen to the change in lung volume during standing and
lying were derived from measurements of the change in the
rib cage and abdomen signals expressed as a percentage of
the change in the sum of the two signals.

Statistics. The occurrence of tonically active units and
units with postinspiratory discharge was compared between
standing and lying with a \( \chi^2 \) test with a Yates correction
for continuity. The discharge frequencies of single motor units
and the respiratory variables were not distributed normally
and are expressed as median and interquartile (IQ) range
with each single motor unit represented only once by the
average frequencies derived from three consecutive breaths.
Therefore, statistical tests based on ranks were used. A
two-way ANOVA on ranks was performed with VT
between standing and lying. For motor unit firing rates, an
two-way ANOVA on ranks was used to compare variables
Therefore, statistical tests based on ranks were used. A
Mann-Whitney rank-sum tests were performed on data for compar-
isons within individual subjects between standing and lying
and to compare initial discharge frequencies for units re-
cruited before and after the onset of rib cage and abdominal
expansion. A Student’s \( t \)-test was used to compare end-tidal
CO\(_2\) data. All analyses were conducted using SigmaStat
(version 2.0) except the ANOVA with covariates, which was
performed with SPSS (version 7.5).

RESULTS

For the diaphragm, in six subjects, activity from 182
single motor units was recorded during standing and
from 159 single motor units during lying. For the
parasternal intercostal muscles, in five subjects, activity
from 116 single motor units was recorded during standing
and from 124 single motor units during lying.
The median number of units in each subject in each
posture for each muscle was 28 (range 16–38). The
recordings were well tolerated and without complica-
tion.

Of the 341 motor units in the diaphragm, only 11
units (3%) discharged tonically throughout the respira-	ory cycle, whereas 14 of 240 units (6%) in the
parasternal intercostals discharged tonically. All
the tonically active units in the diaphragm and most in the
parasternal intercostals were recorded during lying
(Table 1). All but two of the tonically active units
increased their discharge with inspiration by \( \sim \)6 Hz
(from a mean initial discharge frequency of 5.3 to a
mean final discharge frequency of 11.0 Hz). Table 1
also shows the number of units that had pronounced
postinspiratory discharge but were not tonically active
throughout expiration. As with tonic units, the majority
of units with postinspiratory activity were recorded
when the subject was lying supine. The \( \chi^2 \) tests showed
that there were significantly more units with either
tonic or postinspiratory activity during lying (~15% of
units) compared with standing (~4% of units) for both
the diaphragm and the parasternal intercostal muscles
\( P < 0.05 \).

Respiratory variables. Movement of the rib cage (as a
proportion of the sum of rib cage and abdominal expa-
sion) was greater during standing compared with lying.
Conversely, expansion of the abdomen (as a propor-
tion of the sum of rib cage and abdominal expansion)
was greater during lying. Rib cage movement ac-
counted for 65% [60–69%; median (IQ range)] of the
total volume of each breath during standing (median
for each subject ranged from 54 to 84%) but accounted
for only 47% [33–51%] of the total volume of each
breath during lying (\( P < 0.01 \)) (median for each subject
ranged from 21 to 56%). Figure 2 depicts the relative
contribution of rib cage and abdominal expansion to VT
during lying and standing. For the group of subjects,
the ratio of rib cage to abdominal expansion halved
from 1.9:1 during standing to 0.9:1 during lying. These
ratios were similar for both experimental sessions.

There were no significant differences between stand-
ing and lying in major ventilatory variables, including
\( T_i \), \( f \), \( V_T \), \( V_{e} \), or \( V_{e} \), during the experimental sessions
when EMG was recorded from the diaphragm (Table 2).
End-tidal CO\(_2\) was monitored on-line and remained
constant throughout the experimental sessions. In
three subjects, end-tidal CO\(_2\) was measured off line,
and there was no difference between standing and

Table 1. Summary of inspiratory motor units from
diaphragm and parasternal intercostal muscles

<table>
<thead>
<tr>
<th></th>
<th>Diaphragm</th>
<th>Parasternal Intercostals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standing</td>
<td>Lying</td>
</tr>
<tr>
<td>Total no. units</td>
<td>182</td>
<td>159</td>
</tr>
<tr>
<td>Tonic activity</td>
<td>0</td>
<td>11*</td>
</tr>
<tr>
<td>Postinspiratory activity</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Either tonic or postinspiratory activity</td>
<td>6</td>
<td>21*</td>
</tr>
</tbody>
</table>

*Significantly more units during lying compared with standing, \( P < 0.05 \).
lying [6.0 ± 0.2 (SE)% (42.8 ± 1.4 Torr) and 6.1 ± 0.2% (43.5 ± 1.4 Torr), respectively; \( P = 0.47 \)].

During recordings from parasternal intercostal units, ventilation increased during standing from 7.1 l/min (IQ range 5.5–10.2 l/min) to 9.4 l/min (IQ range 8.0–12.7 l/min) and Ti decreased from 1.8 s (IQ range 1.5–2.4 s) to 1.6 s (IQ range 1.3–2.0 s; see Table 2).

Discharge frequencies of diaphragmatic motor units. For the group of subjects, the initial discharge frequency for diaphragmatic motor units during quiet breathing while standing (median 6.9 Hz; IQ range 4.7–9.7 Hz) was not significantly different from that during lying (6.4 Hz; IQ range 4.3–8.4 Hz; Fig. 3).

When the units were divided into those that were recruited before and after the onset of abdominal expansion at the beginning of inspiration, there was again no difference between the initial discharge frequencies. There also remained no difference between lying and standing in the initial discharge frequencies of units recruited before and after the onset of rib cage expansion. However, the final discharge frequencies of the diaphragmatic motor units across subjects was higher [by 1 Hz (12%); \( P < 0.05 \)] when subjects were standing (9.1 Hz; IQ range 7.6–11.3 Hz) compared with lying (8.1 Hz; IQ range 6.6–10.3 Hz; Fig. 3).

Because of the difference in final discharge frequencies for the group data, we subsequently analyzed data from individual subjects to determine whether the increases in motor unit discharge frequencies were associated with increases in ventilation. Only two of the six subjects had a significant increase in final discharge frequencies of diaphragmatic motor units during standing, and, in one of these subjects, the initial discharge frequencies also increased. The subject who

<table>
<thead>
<tr>
<th>Ventilatory Variables</th>
<th>Diaphragm Standing</th>
<th>Lying</th>
<th>Parasternal Intercostals Standing</th>
<th>Lying</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial frequency, Hz</td>
<td>6.9 (4.7–9.7)</td>
<td>6.4 (4.3–8.4)</td>
<td>7.0 (5.6–8.4)</td>
<td>6.4 (4.8–8.7)</td>
</tr>
<tr>
<td>Final frequency, Hz</td>
<td>9.1 (7.6–11.3)*</td>
<td>8.1 (6.6–10.3)</td>
<td>8.0 (6.6–9.9)</td>
<td>8.4 (7.0–10.3)</td>
</tr>
<tr>
<td>Ti, s</td>
<td>1.5 (1.3–1.8)</td>
<td>1.6 (1.4–1.9)</td>
<td>1.6 (1.3–2.0)</td>
<td>1.8 (1.5–2.4)*</td>
</tr>
<tr>
<td>f, breaths/min</td>
<td>16.1 (14.5–17.3)</td>
<td>15.2 (12.4–18.0)</td>
<td>16.2 (13.6–19.3)</td>
<td>14.0 (12.0–16.2)</td>
</tr>
<tr>
<td>Vt, ml</td>
<td>628 (467–740)</td>
<td>638 (465–821)</td>
<td>642 (530–777)</td>
<td>548 (458–658)</td>
</tr>
<tr>
<td>Vt/Ti, ml/s</td>
<td>339 (291–405)</td>
<td>395 (256–452)</td>
<td>375 (293–505)</td>
<td>294 (214–495)</td>
</tr>
<tr>
<td>Ve, l/min</td>
<td>8.6 (7.0–11.0)</td>
<td>9.3 (6.5–11.4)</td>
<td>9.4 (8.0–12.7)*</td>
<td>7.1 (5.5–10.2)</td>
</tr>
<tr>
<td>VT, ml</td>
<td>626 (467–740)</td>
<td>638 (465–821)</td>
<td>642 (530–777)</td>
<td>548 (458–658)</td>
</tr>
<tr>
<td>VT/TI, ml/s</td>
<td>339 (291–405)</td>
<td>395 (256–452)</td>
<td>375 (293–505)</td>
<td>294 (214–495)</td>
</tr>
<tr>
<td>V̇E, l/min</td>
<td>8.6 (7.0–11.0)</td>
<td>9.3 (6.5–11.4)</td>
<td>9.4 (8.0–12.7)*</td>
<td>7.1 (5.5–10.2)</td>
</tr>
</tbody>
</table>

Values are medians with interquartile range in parentheses from 6 subjects during recordings from diaphragm and parasternal intercostal muscles in standing and lying postures. Ti, inspiratory time; f, breathing frequency; Vt, tidal volume; Vt/Ti, mean inspiratory flow; Ve, minute ventilation. Diaphragm and parasternal intercostal recordings were obtained in separate experimental sessions. *Significantly higher values between standing and lying, \( P < 0.05 \).
had increases in both initial and final discharge frequencies during standing increased her \( V_T \) (by 32%) and \( V_T/TI \) (by 28%) during standing (subject 1, Fig. 4). The other subject with increased final discharge frequencies for diaphragmatic motor units increased \( V_T \) (by 9%) and \( V_T/TI \) (by 7%), but the changes in \( V˙E \) were not significant.

Parasternal intercostal single motor unit discharge frequencies. For the group data from the parasternal intercostal muscles, the initial discharge frequency during standing (7.0 Hz; IQ range 5.6–8.4 Hz; Fig. 5) was not significantly different from that during lying (6.4 Hz; IQ range 4.8–8.7 Hz). As for the diaphragm, there were no significant differences between the initial discharge frequencies of motor units that were recruited before or after the onset of rib cage expansion during standing and lying. For units recruited after the onset of rib cage expansion, there were no differences in initial firing frequencies between standing and lying. In contrast to the diaphragm, there was no significant difference between the median final discharge frequencies of the parasternal units when subjects were standing and lying [8.0 Hz (IQ range 6.6–9.9 Hz) and 8.4 Hz (IQ range 7.0–10.3 Hz), respectively].

Analysis of the data from individual subjects also showed no difference between the final discharge frequencies during standing and lying for any subject. One subject had increased initial discharge frequencies during standing. Even for the two subjects who increased \( V_T/TI \) (by 21 and 37%) during standing, there was no increase in motor unit discharge frequency (Fig. 4).

**DISCUSSION**

There were two major findings from this study. First, there was little change in inspiratory motor unit discharge frequencies between the lying and standing postures. The discharge frequency of diaphragm but not of parasternal motor units increased by \( \sim 12\% \) during standing for the group. However, on the basis of data from single subjects, some of this increase may be accounted for by an increase in \( V_T \) and \( V_T/TI \). Second, inspiratory motor units were more likely to discharge tonically throughout expiration or to have postinspiratory activity during lying than standing (15% of units compared with 4%).

**Thoracoabdominal motion.** Expansion of the abdomen during breathing is often used to estimate the extent to which the diaphragm contributes to lung volume (32, 37). When posture is changed from standing to lying, the ratio of rib cage to abdominal expansion halves (Ref. 47; confirmed in the present study). During standing, diaphragmatic contraction increases abdominal pressure and thereby expands the rib cage via the zone of apposition (25), so that the prominent rib cage expansion during standing could be partly driven by diaphragmatic contraction. Alternatively, other obligatory inspiratory muscles acting on the chest wall may contribute more during standing to increase rib cage stiffness, but this may not involve the parasternal intercostal muscles.

In the standing position, FRC increases and the diaphragm is at a shorter muscle length (14). Despite this apparent length-tension disadvantage, gastric and transdiaphragmatic pressure twitches (produced by stimulation of the phrenic nerves) increase by only \( \sim 2 \) cmH\(_2\)O in the sitting compared with the supine posture (38). However, with sitting, esophageal pressure (produced by phrenic nerve stimulation at rest) decreased by \( \sim 20–30\% \) compared with lying supine. This results in a 50% increase in the ratio of the gastric-to-esophageal twitch pressure (38) and suggests a decreased ability of the diaphragm to generate volume with sitting compared with lying. Stimulated contractions of the diaphragm in patients with high-level quadriplegia (i.e., without the use of abdominal muscles) produce significantly higher inspired volumes in the supine compared with sitting posture (15). However, the inspired volume in these patients can be approximately doubled during upright postures by compression of the
abdomen (15, 45). It is not known how esophageal pressure twitches change when healthy subjects stand upright unsupported. It may be that in standing, with intact and active abdominal muscles (17), the same VT may be generated without increased drive to the diaphragm even though it is at a shorter muscle length. The efficiency of the diaphragm may be compensated for by changes in the stiffness of the rib cage and the abdomen due to changes associated with the activation of other inspiratory, abdominal, and pelvic floor muscles, but this cannot be determined from the present experiment.

**Tonic and postinspiratory units.** The significantly higher fraction of motor units in both the diaphragm and the parasternal intercostal muscles that showed tonic or postinspiratory activity while the subjects were supine suggests that in this posture the thorax experiences a net expiratory load. The extra activity in inspiratory muscles during expiration while the subjects were lying would act to minimize the decrease in FRC, reduce airway closure, and slow expiration. The diaphragm is lengthened in the supine posture by rostral displacement of the abdominal contents. This passive lengthening of the diaphragm may increase muscle spindle discharge and hence facilitate motor unit activity of the diaphragm and, possibly, other inspiratory muscles via spinal or supraspinal pathways (10, 39). Alternatively, increased muscle spindle activation may occur in parasternal muscles in the supine posture during expiration. Although the resting length of these muscles in dogs is longer in the upright posture, the shortening of parasternal intercostal muscles during inspiration and their passive lengthening during expiration are greater when supine (40).

**Diaphragmatic activity.** During standing, the diaphragm is lower in the chest, presumably due to the effects of gravity on the abdominal contents. FRC is elevated during standing compared with lying (e.g., Refs. 7, 14, 44), and, as the muscle length is shorter, the diaphragm is at a less advantageous position on its length-tension curve. In contrast, when subjects are lying supine, the abdominal contents displace the passive diaphragm to a longer resting length (48, 49). Simple models of diaphragm mechanics would predict that diaphragmatic activation should increase between lying and standing to maintain VT. The increased load on the contracting diaphragm during standing has been proposed to require a compensatory reflex (such as a stretch reflex) that increases muscle activation and maintains VT despite changes from supine to the upright posture (7, 8, 28, 41, 42). The evidence for this view was derived from studies of diaphragmatic EMG that showed an increase in activity in the upright compared with supine posture in humans (20, 35) and in animals (12, 22, 46). Some of these studies suggested a role for phrenic afferents sensitive to changes in diaphragmatic tension and operating length (12, 22). However, some of the evidence in humans may be flawed. The decrease in end-expiratory length of the diaphragm in the standing posture, compared with the supine posture, produces an artifactual increase in amplitude of diaphragmatic EMG measured with bipolar esophageal electrodes (Ref. 24; see also Refs. 2, 3, 33, 34). Doubts have also been cast on some of the data.

Fig. 5. Discharge frequencies for parasternal intercostal muscle motor units during standing and lying. Histograms are of initial (left) and final (right) discharge frequencies for the units in parasternal intercostal muscles during standing (A) and lying (B). Each observation is from the behavior of a single motor unit averaged over 3 breaths during quiet breathing. Median discharge frequencies are shown. There were no significant differences in frequencies between standing and lying.
from animals because an artifact related to muscle length changes was observed with intramuscular electrodes in the dog (6). Because of these difficulties, a more direct measure of neural drive to the diaphragm was used in the present study.

Discharge frequencies. Direct measurements of changes in drive to the diaphragm can be made by measuring changes in the discharge frequency of single motor units. However, contraction of the diaphragm is achieved by increases in both the number of motor units recruited and their discharge frequency (9, 19, 29). Although the number of motor units studied was similar between standing and lying and the same number of recording sites was examined, our techniques were not designed to detect changes in the number of motor units recruited between lying and standing. Therefore, it is possible that an increase in drive may have been translated preferentially into increased recruitment of motor units with only a small increase in discharge frequency. However, it is very unlikely that recruitment would occur exclusively without a concomitant increase in discharge frequencies of those motor units already recruited. An increase in the final discharge frequency of diaphragmatic single motor units occurs with increases in both \( V_T/T_i \) and inspired volume in both cats (29) and humans (9). With eightfold increases in inspiratory flow or lung volume, discharge frequencies for the human diaphragmatic motor units increase from \(~8\) Hz to 11 Hz (9), but in patients with chronic obstructive pulmonary disease (COPD) the discharge frequency can increase up to 18 Hz during tidal breathing (18). Compared with the four- to fivefold increases in diaphragmatic EMG reported in the literature (20), and the high motor unit discharge frequencies in COPD patients, the changes we have found are small and inconsistent. In the majority of subjects, there was no increase in motor unit discharge frequency during standing for either the diaphragm or the parasternal intercostal muscles.

Initial discharge frequencies of diaphragmatic single motor units also increase as inspiratory flow and hence inspiratory drive increase (9), but, in the present study, there was no difference between the initial discharge frequencies during standing and lying for either the diaphragm or parasternal intercostal muscles. There were also no differences between the initial discharge frequencies for units recruited either before or after the onset of rib cage or abdominal expansion during standing or lying. If a load-compensating reflex facilitated diaphragm or parasternal intercostal activity during standing, then initial discharge frequencies should be higher after the onset of the load compared with before the onset of rib cage or abdominal expansion. These findings also support the conclusion that any change in drive between the two postures is small.

Some subjects increased \( V_T \) and inspiratory flow during standing, possibly due to an increase in metabolic demand. If \( CO_2 \) production is increased during standing, there will be a reflex increase in the neural drive to breathe and therefore increased ventilation during standing that would act to return \( CO_2 \) to normal levels. One of these subjects increased the discharge frequency of diaphragmatic motor units, but in no subject was there a change in the discharge frequency of parasternal intercostal motor units. The tendency in individual subjects to increase diaphragmatic but not parasternal intercostal motor unit discharge rates is not unexpected. When ventilatory drive is increased, as in patients with COPD, or in normal subjects exposed to increased chemical drive, the increase in discharge rates of motor units is greater for the diaphragm than those for the parasternal intercostals (170 and 130%, respectively; Refs. 18, 23, 26).

The reasons for the lack of parallel increase in motor unit discharge frequencies between the diaphragmatic and the parasternal intercostal motor units when ventilatory drive increases under different conditions are not clear. There may be a bias in favor of the diaphragm in the distribution of increased drive to inspiratory muscles. Alternatively, increases in drive to phrenic motoneurons may be more readily converted into increases in motor unit discharge rate than for the parasternal intercostal motoneurons. With immersion of the abdomen, activity decreases in both human diaphragm and parasternal intercostal muscles (41). Therefore, it appears that a change in effective inspiratory drive is distributed in parallel to these two inspiratory muscles.

Overall, the results are consistent with the concept that the diaphragm acts principally as a flow generator (because it has a great ability to shorten isotonically) rather than as a pressure generator (1, 43). The change in transdiaphragmatic pressure is reduced during exercise, although ventilation increases (43), probably because the other inspiratory muscles expand the rib cage during inspiration (1, 43). We suggest that, although the length of the diaphragm decreases between lying supine and standing, the diaphragm does not require a major increase in neural drive to achieve the same \( V_T \) during eupnea.

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REFERENCES


