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Hudson AL, Butler JE, Gandevia SC, De Troyer A. Role of the diaphragm in trunk rotation in humans. *J Neurophysiol* 106: 1622–1628, 2011. First published July 13, 2011; doi:10.1152/jn.00155.2011.—The objectives of the present study were to test the hypothesis that the costal diaphragm contracts during ipsilateral rotation of the trunk and that such trunk rotation increases the motor output of the muscle during inspiration. Monopolar electrodes were inserted in the right costal hemidiaphragm in six subjects, and electromyographic (EMG) recordings were made during isometric rotation efforts of the trunk to the right ("ipsilateral rotation") and to the left ("contralateral rotation"). EMG activity was simultaneously recorded from the parasternal intercostal muscles on the right side. The parasternal intercostals were consistently active during ipsilateral rotation but silent during contralateral rotation. In contrast, the diaphragm was silent in the majority of rotations in either direction, and whenever diaphragm activity was recorded, it involved very few motor units. In addition, whereas parasternal inspiratory activity substantially increased during ipsilateral rotation and decreased during contralateral rotation, inspiratory activity in the diaphragm was essentially unaltered and the discharge frequency of single motor units in the muscle remained at 13–14 Hz in the different postures. It is concluded that *1*) the diaphragm makes no significant contribution to trunk rotation and *2*) even though the diaphragm and parasternal intercostals contract in a coordinated manner during resting breathing, the inspiratory output of the two muscles is affected differently by voluntary drive during trunk rotation.

posture; inspiratory drive; voluntary contraction; motoneurons

THE MECHANICS of a skeletal muscle is essentially determined by the anatomy of the muscle and the structures it displaces when it contracts. Given that the muscle fibers of the costal portion of the diaphragm run cranially and dorsally from their insertion on the lower ribs, it would therefore be expected that isolated contraction of one hemidiaphragm would both lift these ribs and pull them backward relative to the upper ribs. In addition, even though the diaphragm is the main inspiratory muscle, it receives corticospinal inputs (e.g., Gandevia and Rothwell 1987; Murphy et al. 1990) and is involved in a range of nonrespiratory contractions, such as stabilization of the trunk prior to rapid arm movements (Hodges et al. 1997), flexion of the upper and lower extremities (Kolar et al. 2010), and trunk extension (in patients with complete cervical spinal cord injury, Sinderby et al. 1992; see also Hodges et al. 2001). On these grounds, we hypothesized that the muscle would participate in ipsilateral rotation of the trunk. Thus the right hemidiaphragm would contract during rotation of the trunk to the right to pull the lower rib cage on the right side dorsally relative to the spine, whereas it would remain silent during rotation of the trunk to the left (contralateral rotation). Conversely, the left hemidiaphragm would contract during rotation of the trunk to the left to pull the lower rib cage on the left side dorsally relative to the spine.

In addition, the parasternal intercostal muscles (the intercartilagenous portion of the internal intercostals) are obligatory inspiratory muscles (e.g., De Troyer and Sampson 1982; Gandevia et al. 2006), and we showed in a recent study that these muscles contract during ipsilateral rotation of the trunk (Hudson et al. 2010). More importantly, although the muscles were active during inspiration in all trunk postures, their inspiratory output increased during ipsilateral rotation but decreased during contralateral rotation (Hudson et al. 2010). It is well established in the dog that activation of the diaphragm and parasternal intercostals during inspiration are governed by similar control mechanisms (De Troyer 1991, 1997). The observation that the amount of inspiratory activity recorded from the parasternal intercostals increases when healthy individuals attempt to breathe with the diaphragm alone (De Troyer and Sampson 1982; Fitting et al. 1988) suggests that this principle may also apply to humans. Therefore, we also hypothesized that inspiratory activity in a particular hemidiaphragm would increase during ipsilateral rotation of the trunk and decrease during contralateral rotation.

To test these hypotheses, we inserted needle electrodes into the costal portion of the right hemidiaphragm in healthy subjects performing isometric rotation efforts of the trunk. Recordings were simultaneously obtained from the parasternal intercostals on the right side of the sternum. Therefore, the relative contributions of the two muscles to rotation could be evaluated. In addition, as the subjects breathed quietly with the trunk rotated to the right or left as well as in the neutral position, the discharge frequencies of large numbers of inspiratory single motor units in the diaphragm were compared. Consequently, the effect of rotation on the motor output of the diaphragm during inspiration could also be assessed.

METHODS

The studies were carried out in six healthy men aged 34–60 yr. The subjects gave informed written consent to the procedures, which conformed with the Declaration of Helsinki and were approved by the Human Research Ethics Committee of the University of New South Wales. Two subjects were aware of the rationale behind the study, but the other four were not. Before the study, these subjects were just told that the purpose was to obtain electromyographic (EMG) recordings from the diaphragm during breathing and during trunk rotation.

Experimental setup. The experimental setup was similar to that used to study the effect of trunk rotation on neural drive to the

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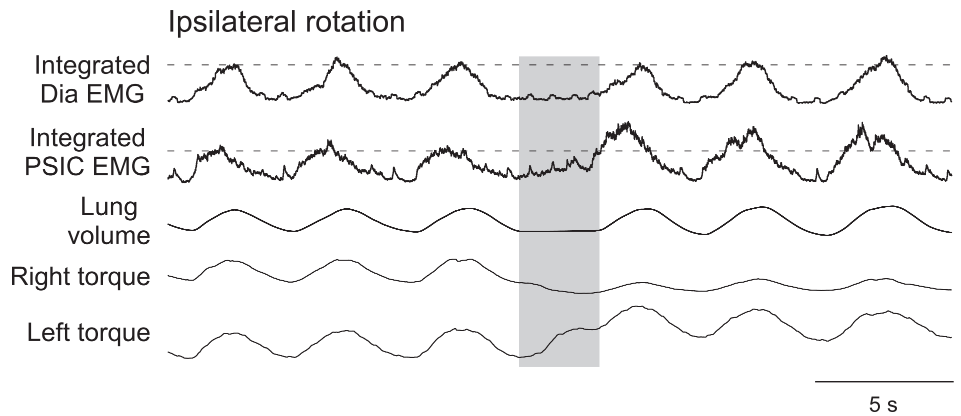

Fig. 1. Typical multiunit recordings from the diaphragm and parasternal intercostal muscles during respiration and trunk rotation. From *top* to *bottom*, integrated diaphragm (Dia) EMG, integrated parasternal intercostal (PSIC) EMG, lung volume, and the torque from load cells below the right and left clavicle are shown. Vertical calibration: 0.5 liter for lung volume and 1 Nm for torque. During the apneic period of ipsilateral rotation (gray shaded region) there was no activity in the diaphragm, but activity was induced in the parasternal intercostal muscle. During breathing with a maintained ipsilateral rotation (on *right*) the amount of diaphragm activity is similar to that during breathing in the neutral position. In contrast, the amount of inspiratory activity from the parasternal intercostal muscles is greater.

parasternal intercostal muscles (Hudson et al. 2010). Subjects were seated in a chair that had been modified so that the torque developed during isometric rotation efforts of the trunk toward the right and the left could be measured. Tension-compression load cells (Xtran, Melbourne, Australia) were attached to rigid supports on the chair, which extended over both shoulders of the subject (see Fig. 1*A* in Hudson et al. 2010). The load cells were positioned firmly ~2 cm below the level of the clavicle, ~11 cm from the midline on the right and left sides. To rotate to the right, the subject made an isometric contraction against the load cell below the left clavicle, and for a rotation to the left, the subject made an isometric contraction against the load cell below the right clavicle. For brevity, isometric rotation efforts are hereafter referred to as "rotations." Subjects were specifically instructed to relax their shoulders and keep the pectoral muscles quiescent during rotations. The strength of rotations is presented as torque (Nm). It is calculated from the force applied to the load cells and the distance (on the right or left) from the midline measured in each subject. The maximal voluntary rotary torque developed during isometric rotation to the left was measured in each subject and averaged 17.9 ± 3.2 Nm (mean ± SE) for the six subjects.

Subjects breathed through a mouthpiece connected to a pneumotachograph (3700 series, Hans Rudolph), and the signal of airflow was integrated to give the changes in lung volume. Subjects had visual feedback of lung volume and force from both load cells. EMG activity was recorded from both the diaphragm and the parasternal intercostals on the right side of the chest to ensure that the rotations in this study were performed similarly to those in our previous study (Hudson et al. 2010) and to have a direct comparison between the responses of the two muscles to rotation. Therefore, in each subject a pair of surface electrodes (Ag-AgCl; 10-mm diameter; Cleartrace, ConMed, Utica, NY) was attached to the skin overlying the parasternal intercostals in the first and second interspaces, 1–2 cm lateral to the sternum.

The method for recording intramuscular EMG from the diaphragm has been described previously (Butler et al. 1999; De Troyer et al. 1997; Gandevia et al. 1999). The diaphragm on the right side was visualized in each subject with a 12–5 MHz ultrasound linear probe (Phillips iU22, Bothell, WA) to determine the precise location and depth for electrode insertion. The location for recording was in the zone of apposition of the diaphragm in the midclavicular line. The approach for needle insertion was through the 7th or 8th intercostal space, judged on individual anatomy. The depth of the internal edge of the diaphragm relative to the skin surface ranged between 21 and 32 mm, and the maximal possible length was marked on the electrode for each subject. A small dose of local anesthetic (1–2 ml; lignocaine 1%) was injected along the track planned for electrode insertion ~10 min prior to recordings.

Recordings were made with a Teflon-coated monopolar electrode (Medelec DMG50, Old Woking, UK) and were referenced to a

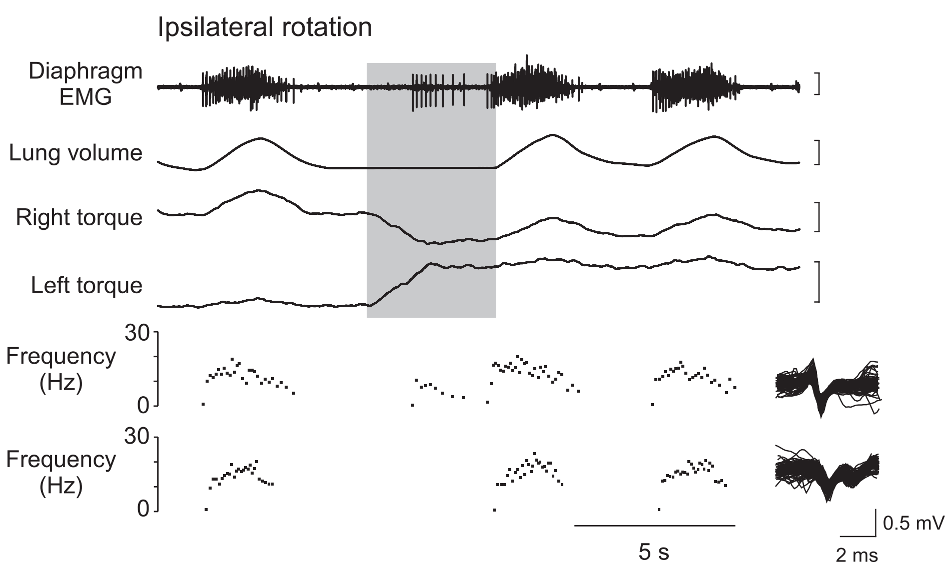

Fig. 2. Representative recording of single motor unit activity in the diaphragm during ipsilateral trunk rotation and inspiration. From *top* to *bottom*, multiunit diaphragm EMG, lung volume, the torque from right and left load cells, and the instantaneous discharge frequencies of 2 single motor units from this recording are shown. Superimposed action potentials are shown on *right*. Vertical calibration: 0.5 mV for EMG, 0.5 liter for lung volume, and 1 Nm for torque. Single motor unit activity in the diaphragm during the apneic period of ipsilateral rotation (gray shaded region) was present in 9 of 64 rotations and always limited to a single motor unit. All units that discharged in rotation were also active in inspiration. The same diaphragm single motor units discharge with comparable peak inspiratory discharge rates in the neutral position and during ipsilateral rotation.

surface electrode positioned 2–3 cm away. The needle was inserted perpendicular to the skin surface and advanced in small steps through the intercostal muscles and into the diaphragm. EMG activity was continuously monitored on a loudspeaker and an oscilloscope throughout the procedure. Once a site in the diaphragm was encountered that contained single motor unit activity with an acceptable signal-to-noise ratio (>3:1) during quiet breathing, the loudspeaker audio signal was removed. The experimenter inserting the needle electrode had continual audio feedback through headphones. After completion of the experimental protocol (see below), the needle was moved to a different site within the muscle. In each subject, five to nine sites were studied.

All signals were stored on computer via a Cambridge Electronic Design 1401 interface (Cambridge, UK) for subsequent analysis. Diaphragm EMG was sampled at 10 kHz, parasternal intercostal EMG at 5 kHz, and airflow, volume, and force at 1 kHz. EMG signals were amplified and band-pass filtered below 53 Hz and above 3,000 Hz for the diaphragm and below 53 Hz and above 1,000 Hz for parasternal intercostal recordings.

Experimental protocol. Diaphragm and parasternal intercostal EMG activity was recorded first during a period of quiet breathing in a "neutral" position. The neutral position was a forward-facing posture in which the subject was relaxed, with the shoulders square to the hips. Then, under instruction from an experimenter, the subject remained apneic for a few seconds at end expiration and made a rotation of the trunk about the vertical axis to either the right or the left. After the rotation was achieved, the subject resumed quiet breathing for ~30 s while maintaining a constant rotational torque. The subject then relaxed (i.e., resumed the neutral position). Sometimes, during rotation, the diaphragm recording site no longer contained crisp single motor unit activity (identified by visual inspection or from the audio feedback to the experimenter inserting the needle electrode) because of slight electrode movement. In this circumstance, the electrode was moved to a new recording site that contained inspiratory single motor unit activity while the subject maintained the rotation. After a period of quiet breathing with this new recording site, the subject then relaxed to the neutral position. This protocol allowed us to record from large numbers of single motor units in the diaphragm both with the trunk in the neutral position and with the trunk rotated to the right and to the left. As recordings were made from the diaphragm and parasternal intercostal muscles on the right side, rotations to the right represent ipsilateral rotations and rotations to the left represent contralateral rotations. For the six subjects, a total of 64 ipsilateral rotations and 57 contralateral rotations were recorded.

Frequently, the recording site in the diaphragm was not affected by the rotation, and the same motor units could be seen before and during the rotation. This occurred in 25 ipsilateral rotations and 28 contralateral rotations. For these rotations, the discharge of the same motor units, as well as the multiunit activity of the diaphragm, could be compared directly between neutral and rotated postures.

Data analysis. For each rotation, three breaths recorded in the neutral position before the rotation or after return to neutral ("neutral breaths") and three breaths recorded with the trunk rotated ("rotated breaths") were analyzed. The apneic periods during which rotations were performed (either from the neutral position or return to neutral) were also analyzed. Analysis was made in two stages.

First, the behavior of diaphragm single motor units was examined. This technique has been described previously in detail (e.g., Gandevia et al. 1999; Saboisky et al. 2007). With a commercial software package (Spike 2; Cambridge Electronic Design), trigger levels were set manually to capture all spikes with an appropriate signal-to-noise ratio. They were subsequently recalled and sorted manually into "templates" based on their size and detailed morphology. Using this method, we could follow simultaneously the discharge of up to four single motor units over several consecutive breaths and isometric rotations of the trunk. For each unit, the peak discharge frequency was measured during inspiration. The discharge frequency of motor units active during the rotation was also measured. As mentioned above, the recording site remained stable for some rotations, and therefore inspiratory activity of the same motor units in the neutral position and the rotated posture could be compared directly.

The second stage of analysis examined multiunit EMG activity from the diaphragm and parasternal intercostal muscles. The periods of recording that were considered for the single motor unit analysis were digitally integrated off-line with a leaky integrator (decay time constant 100 ms). The peak integrated signal during inspiration was measured, relative to the signal during the last third of expiration, for neutral breaths and rotated breaths. To allow comparison between subjects, the inspiratory EMG activity in the rotated breaths was then expressed as a percentage of the value obtained in neutral breaths. For the diaphragm, comparison of inspiratory activity between neutral and rotated breaths was made only for rotations in which the recording site was stable (i.e., at least 1 common single motor unit in the neutral and rotated postures). The proportion of inspiratory time (T_I) that the muscle was active in the neutral and rotated breaths was also measured for all recording sites in the diaphragm. Thus, for each breath, T_I was measured from the airflow signal and the time of onset (T_O) of the integrated diaphragm EMG signal was determined to give $(T_I - T_O)/T_I$, the proportion of T_I that the muscle was active. Measurements of tidal volume, mean inspiratory flow, and isometric rotational torque during these breaths were also made. Torque was measured from the load cell at which compression force occurred, i.e., at the left load cell for ipsilateral (right) rotations and at the right load cell for contralateral (left) rotations.

For each recording site, respiratory variables, torque, $(T_I - T_O)/T_I$, discharge rates of diaphragm single motor units, peak parasternal inspiratory EMG activity, and, for stable sites, peak diaphragm inspiratory EMG activity were averaged over the three neutral breaths and over the three rotated breaths recorded from that site. Values obtained were then averaged over all sites for each subject. There was no difference in respiratory variables or $(T_I - T_O)/T_I$ between neutral breaths associated with ipsilateral rotations and neutral breaths associated with contralateral rotations ($P > 0.05$), and thus data were averaged for all neutral breaths in each subject.

Statistics. Group data are presented as means ± SE (except Fig. 3, which shows means ± SD). Student's paired *t*-test was used to compare torque between left and right rotations. One-way repeated-measures analysis of variance (ANOVA) was used to compare respiratory variables, peak inspiratory EMG activity, $(T_I - T_O)/T_I$, and the peak discharge rate of diaphragm single motor units between breaths

Table 1. *Pattern of breathing and inspiratory muscle activity during EMG recordings in three trunk postures*

	Contralateral Rotation	Neutral	Ipsilateral Rotation
Torque, Nm	1.02 ± 0.11		1.14 ± 0.13
V_T, liter	0.62 ± 0.04	0.63 ± 0.03	0.60 ± 0.03
T_I, s	1.83 ± 0.27	1.76 ± 0.19	1.79 ± 0.23
V_T/T_I, s^{-1}	0.36 ± 0.03	0.37 ± 0.03	0.35 ± 0.03
Diaphragm $(T_I - T_O)/T_I$, %	95.0 ± 2.1	95.7 ± 1.9	96.5 ± 2.1*
Diaphragm activity, %	103.0 ± 2.0		109.5 ± 4.1
PSIC activity, %	83.4 ± 3.8		152.1 ± 11.4†
Discharge frequency, Hz	13.4 ± 0.8	13.2 ± 0.7	13.8 ± 0.7

Values are means ± SE for 6 subjects during quiet breathing in the neutral position and during quiet breathing while a contralateral or ipsilateral rotation of the trunk was maintained. The torque of rotations, tidal volume (V_T), inspiratory time (T_I), mean inspiratory flow (V_T/T_I), the proportion of inspiratory time that the diaphragm was active [$(T_I - T_O)/T_I$], the amount of inspiratory activity measured from the integrated diaphragm and parasternal intercostal muscle (PSIC) EMG signals relative to the amount in the neutral position, and the discharge frequency of populations of diaphragm single motor units recorded in the 3 postures are shown. *$P < 0.05$, †$P < 0.01$, significantly different from recordings during contralateral rotation.

in the neutral position, right rotations, and left rotations. Multiple comparison testing of the mean values was performed, when appropriate, with the Tukey post hoc procedure. Comparison of the discharge rate of motor units that were active in both neutral and rotated breaths was made with Student's paired *t*-test. The criterion for statistical significance was taken as $P < 0.05$.

RESULTS

Representative recordings of multi-motor unit and single motor unit activity recorded from the diaphragm and parasternal intercostal muscles during quiet breathing in a neutral position and during quiet breathing during ipsilateral rotations of the trunk are shown in Figs. 1 and 2. The torque developed during ipsilateral rotary efforts in the six subjects was 1.1 ± 0.1 Nm (range 0.5–2.0 Nm), similar to that for contralateral rotations (1.0 ± 0.1 Nm, range 0.3–1.7 Nm; $P > 0.05$). As shown in Table 1, tidal volume, T_I, and mean inspiratory flow were similar in all postures ($P > 0.05$).

Diaphragm activity during rotation. Each subject showed EMG in the parasternal intercostals during the apneic period of every ipsilateral rotation (Fig. 1; see also Hudson et al. 2010). In contrast, the diaphragm remained silent in the majority of ipsilateral rotations. Diaphragm EMG was present in only 16 of 64 rotations in five subjects, and this activity was of very low amplitude or limited to a single motor unit, as shown in Fig. 2. The average discharge rate of nine single motor units that could be discriminated in these rotations was 7.6 ± 0.4 Hz.

Activity in the diaphragm was even more uncommon in contralateral rotations. Only two motor units in two subjects discharged during the apneic period of these rotations, and these two units were among those that discharged during ipsilateral rotation. These common units discharged at 7.7 and 6.5 Hz in contralateral rotation compared with 5.0 and 7.4 Hz, respectively, in ipsilateral rotation. All motor units active in the apneic period of rotation discharged in inspiration.

Effect of rotation on diaphragm inspiratory single motor unit activity. All of the 344 single motor units in the diaphragm discharged phasically with inspiration, except one unit that had inspiratory modulation of tonic activity during maintained ipsilateral rotation. The peak inspiratory discharge rates of all

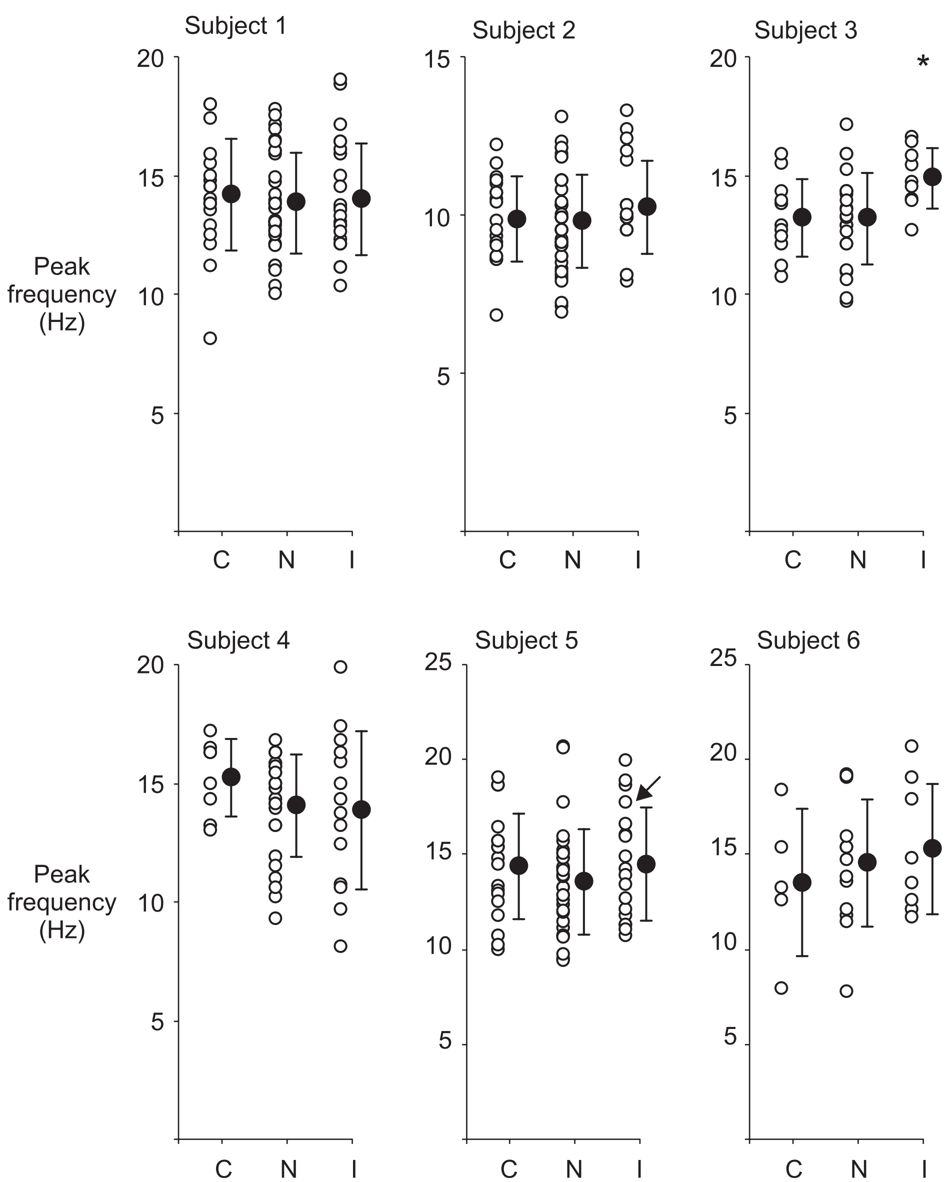

Fig. 3. Peak inspiratory discharge rate of populations of diaphragm single motor units recorded in neutral and rotated postures. The peak inspiratory discharge rate of motor units (open circles) recorded from each subject ($n = 6$) during breathing in 3 conditions is shown: during contralateral rotation (C), in a neutral position (N), and during ipsilateral rotation (I). Average (±SD) data for each posture are shown as filled circles (see Table 1 for group data). There was no difference in the peak inspiratory discharge rate of diaphragm motor units between the 3 postures in 5 of 6 subjects. The arrow indicates the 1 motor unit that had inspiratory modulation from a background tonic level during maintained ipsilateral rotation. *Significantly different from the neutral position ($P < 0.05$).

diaphragm motor units recorded in the neutral, contralateral, and ipsilateral postures for each individual subject are shown in Fig. 3. For the group of subjects, the discharge rate for the population of motor units in the neutral position was, on average, 13.2 ± 0.7 Hz (n = 170) and the discharge rates for the motor units recorded during contralateral rotation (13.4 ± 0.8 Hz, n = 80) and those recorded during ipsilateral rotation (13.8 ± 0.7 Hz, n = 94) were no different ($P > 0.05$).

There was also no difference in inspiratory peak discharge rate of the motor units that were identified in both neutral and contralateral postures (Fig. 4, *left*). The inspiratory discharge rate of these common units (n = 51) was 13.3 ± 0.8 Hz in the neutral position and 13.5 ± 0.9 Hz during contralateral rotation ($P > 0.05$). However, there was a small but statistically significant difference in the discharge rate of the units recorded in both neutral and ipsilateral rotations (n = 49). Whereas the inspiratory discharge rate of these units was 13.0 ± 0.8 Hz in the neutral position, it was 13.9 ± 0.8 Hz during ipsilateral rotation ($P < 0.05$; Fig. 4, *right*).

Multiunit inspiratory activity in rotated postures. Inspiratory activity was recorded from the diaphragm and parasternal intercostal muscles in all periods of quiet breathing in both neutral and rotated postures. In agreement with our previous intramuscular recordings (Hudson et al. 2010), the peak parasternal inspiratory activity during ipsilateral rotation was 152.1 ± 11.4% of that in the neutral position (Fig. 1), significantly greater than the peak parasternal inspiratory activity during contralateral rotation, which was 83.4 ± 3.8% ($P < 0.01$). In contrast, even though diaphragm activity commenced slightly earlier during ipsilateral rotation than during contralateral rotation ($P < 0.05$), peak inspiratory activity showed no significant alterations during either ipsilateral or contralateral rotation (P = 0.09) (see Table 1).

DISCUSSION

The main findings of the present study are, first, that rotation of the trunk in either the ipsilateral or the contralateral direction is performed with minimal activity in the costal portion of the diaphragm and, second, that inspiratory activity in the costal diaphragm remains essentially unchanged during breathing with the trunk rotated. In contrast, the parasternal intercostal muscles contract during ipsilateral rotation and show an increase in inspiratory activity, whereas during contralateral rotation they remain silent and show a decrease in inspiratory activity. These differences between the diaphragm and parasternal intercostals have implications for the control mechanisms of the two muscles and for the integration of voluntary and inspiratory drive to them.

Diaphragm in trunk rotation. Because the muscle fibers of the costal portion of the diaphragm run in a cranial-dorsal direction from their insertions on the lower ribs, it would be expected that its contraction, for example, on the right side, would both lift the lower ribs and pull them in a dorsal direction relative to the spine. On this basis, our hypothesis was that the costal diaphragm might participate in ipsilateral rotation of the trunk. However, in our subjects, the muscle usually remained silent during both ipsilateral and contralateral rotation, and whenever ipsilateral rotation elicited diaphragm activity it involved only a few motor units. In addition, the majority of those units that discharged during ipsilateral rotation had low-amplitude potentials and discharged at the very onset of the subsequent inspiration. Thus these units had a low threshold for activation and were likely to be innervated by small motoneurons (for review see Binder et al. 1996; Enoka and Stuart 1984; Henneman and Mendell 1981). Taken together, these observations imply that the force exerted by the diaphragm on the ribs during ipsilateral rotation of the trunk is very small, and the finding that some of the motor units that discharged during ipsilateral rotation also discharged during contralateral rotation further supports this idea. Indeed, it is difficult to provide any biomechanical explanation as to how the right hemidiaphragm could displace the lower ribs on the right side so as to rotate the trunk to the left.

Trunk rotation and diaphragm inspiratory activity. The respiratory apparatus used in this study had a higher airflow resistance than that used in our previous studies (Butler et al. 1999; De Troyer et al. 1997; Gandevia et al. 1999; Saboisky et al. 2007). As a result, when our subjects were breathing

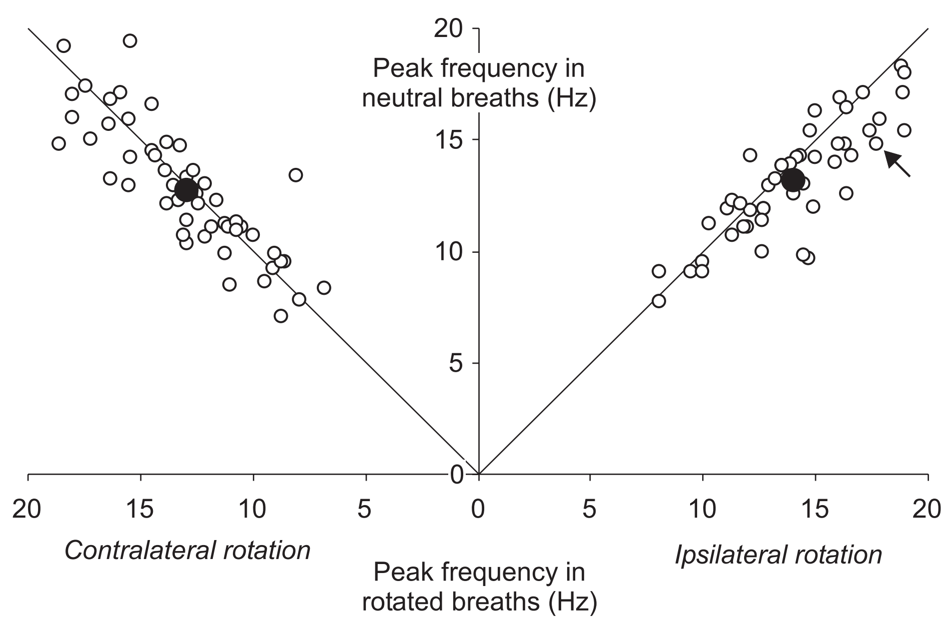

Fig. 4. Comparison of the peak inspiratory discharge rate of motor units active in both neutral and rotated postures. Data from inspiratory single motor units (open circles) that were active in both breathing in a neutral position and breathing during rotation are shown, with mean (± SE) values shown as filled circles. The average peak discharge frequency during breathing in rotated postures is plotted against the corresponding rate during breathing in the neutral position. The inspiratory discharge rate of common units was similar during contralateral rotations and neutral (n = 51 units, on *left*), whereas for ipsilateral rotations the discharge rate was slightly higher in rotated breaths and most points fall below the line of identity (n = 49 units, on *right*). The arrow indicates the 1 motor unit that discharged phasically in the neutral position but had inspiratory modulation from a background tonic activity during maintained ipsilateral rotation.

quietly, the firing rate of the diaphragm motor units at peak inspiration was slightly higher than previously measured. However, this discharge rate did not show any change with ipsilateral or contralateral rotation in five of six subjects (see Fig. 3). Those motor units that were recorded both during breathing in the neutral position and during breathing in the presence of an ipsilateral rotation of the trunk did show a statistically significant increase in firing frequency with rotation (0.9 Hz). However, diaphragm motor unit firing rates are known to be very sensitive to increases in neural drive, and during CO_2-induced hyperpnea they increase their discharge rate by 6.7 Hz when ventilation increases threefold, whereas the parasternal intercostal muscles increase their firing rate by only 1.9 Hz (Gandevia et al. 1999). In contrast, in inspiration during ipsilateral trunk rotation, it is the parasternal intercostals that increase firing rate by 3.3 Hz (Hudson et al. 2010) compared with only 0.9 Hz in the diaphragm. This suggests a large increase in drive to the parasternal intercostal muscles compared with the phrenic motoneurons in such rotation. The multiunit recordings are consistent with only a small effect of ipsilateral trunk rotation on the motor output from the diaphragm during inspiration, as the onset of inspiratory activity during ipsilateral rotation was slightly earlier compared with during contralateral rotation but no different from the onset of activity in the neutral position.

Integration of postural and inspiratory drives. The parasternal intercostal motoneurons receive projections from the motor cortex and the medulla (e.g., Duffin and Lipski 1987; Hilaire and Monteau 1976), and in our previous study (Hudson et al. 2010) we established that the parasternal motor units that are recruited during ipsilateral rotation of the trunk also discharge during inspiration. We speculated, therefore, that the increase in inspiratory output of the parasternal motoneurons during ipsilateral rotation of the trunk was primarily the result of activity in the corticospinal pathways acting at the spinal interneurons and motoneurons. That is, the postural drive to the parasternal motoneurons during rotation would effectively decrease their threshold for activation during inspiration, so that the inspiratory output of the motoneurons would be increased.

Corticospinal pathways also project to the phrenic motoneurons (e.g., Gandevia and Rothwell 1987; Maskill et al. 1991; Murphy et al. 1990), and, indeed, it is well established that the diaphragm can be activated in voluntary respiratory maneuvers (Gandevia et al. 1990) and nonrespiratory tasks (e.g., Hodges et al. 1997; Kolar et al. 2010; Sinderby et al. 1992). Trunk rotation, however, induced little or no activity in the diaphragm, thus implying that the corticospinal drive to the phrenic motoneurons during this particular maneuver is small, and probably insufficient to greatly alter the activation threshold of the motoneurons during inspiration. Thus, even though the diaphragm and parasternal intercostals contract in a coordinated manner during resting breathing (De Troyer and Sampson 1982; Fitting et al. 1988) and are, by and large, controlled by similar central mechanisms (De Troyer 1991, 1997; Hilaire and Monteau 1976; Lipski et al. 1994), the present observations show that the inspiratory output of the two muscles can be affected differently by activity in the motor cortex during an exclusively voluntary maneuver. These findings are consistent with animal data that have demonstrated common bulbospinal projections to phrenic and intercostal motoneurons for respiration (Hilaire and Monteau 1976; Lipski et al. 1994), but common collaterals from corticospinal axons have not been demonstrated (Rikard-Bell et al. 1985, 1986), and this would allow for independent control of these muscles during voluntary trunk rotation.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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