Interplay Between the Inspiratory and Postural Functions of the Human Parasternal Intercostal Muscles

Anna L. Hudson, Jane E. Butler, Simon C. Gandevia, and Andre De Troyer

INTRODUCTION

Although the respiratory functions of the intercostal muscles have long been controversial, it is now well established that the outer layer, the external intercostals, has an inspiratory function, whereas the inner layer, the internal intercostals, has an expiratory function (for review, see De Troyer et al. 2005). Thus the external intercostals, in particular those situated in the dorsal portion of the rostral interspaces, contract during inspiration, and their contraction elevates the ribs and expands the lung. In contrast, the internal intercostals, particularly those situated in the caudal interspaces, contract during expiration and contribute to lung deflation.

Electromyographic studies in normal humans have shown that the external and internal interosseous intercostals are active not only during breathing but also during axial rotations of the trunk (Rimmer et al. 1995; Whitelaw et al. 1992). Specifically, the external intercostals in the lateral portion of the right side contract when the subject rotates the trunk to the left, whereas they remain silent with rotation of the trunk to the right. Conversely, the internal interosseous intercostals on the right side contract when the trunk is rotated to the right but not when it is rotated to the left. This pattern of activation suggests that the muscles make a real contribution to generation of rotary torque. Indeed because the fibers of the external intercostal in each interspace are oriented obliquely, in the caudoventral direction, from the rib above to the rib below, it would be expected that their contraction on one side would move the upper ribs forward (i.e., anteriorly) and the lower ribs backward (i.e., posteriorly). On the other hand, the fibers of the internal interosseous intercostals run in the caudodorsal direction from the rib above to the rib below, so their contraction should displace the upper ribs backward and the lower ribs forward (see Fig. 4 in Whitelaw et al. 1992).

The intercartilaginous portion of the internal intercostals (the parasternal intercostals) has the same fiber orientation as the interosseous portion of the muscle. However, the parasternal intercostals have an inspiratory rather than expiratory function. Both in animals (De Troyer and Legrand 1995; De Troyer et al. 1996; Legrand et al. 1996a,b) and in humans (De Troyer and Sampson 1982; De Troyer et al. 1998; Gandevia et al. 2006; Saboisky et al. 2007), these muscles have an inspiratory mechanical advantage and are active during inspiration. In anesthetized dogs, the contribution of the parasternal intercostals to the inspiratory rib elevation and lung expansion is, in fact, much greater than that of the external intercostals (De Troyer 1991; De Troyer and Wilson 2000). Yet because the parasternal intercostals and the internal interosseous intercostals have the same fiber orientation, it would be expected that the two muscles would have qualitatively similar roles during trunk rotation. Therefore one would predict that the parasternal intercostals on the right side of the sternum would also contract during rotation to the right and that they would also remain silent during rotation to the left. However, the role of the parasternal intercostals during trunk rotation is not known.

The initial objective of the present study was to test this hypothesis. Thus we measured the pattern of contraction of the parasternal intercostal muscles during isometric rotation efforts of the trunk. In agreement with the hypothesis, the muscles on the right were active during rotations to the right but not during rotations to the left. Therefore we recorded the discharge of single motor units in these muscles to answer the two following questions. First, are the motor units that are active during...
rotation to the right also active during inspiration, or, conversely, are the motor units involved in rotation different from those used in inspiration? Second, how does the contraction of the parasternal intercostals during rotation affect the inspiratory drive to the muscle?

**METHODS**

The studies were carried out in six healthy men aged 27–58 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 had no prior experience in respiratory studies, and although four subjects had previously participated in many respiratory experiments, only two of them were aware of the rationale behind the study. Before the study, the subjects were just told that the purpose was to obtain electromyographic recordings from muscles of the chest wall during quiet breathing and a postural task.

**Experimental setup**

Subjects were seated in a chair, and all restrictive garments were removed. The chair had been modified so that subjects could perform isometric rotations of the thorax both toward the right and the left and that the force developed during rotation efforts could be measured. Thus tension-compression load cells (UMM-K10, Dacell, Korea) were attached to rigid supports on the chair, which extended over both shoulders of the subject (Fig. 1A). In each subject, the load cells were positioned firmly ~2 cm below the level of the clavicle, ~10 cm from the midline on the right and left sides. The maximal voluntary rotary force developed during isometric rotation to the left was measured in each subject, and averaged 16.4 ± 3.0 (SE) Nm for the six subjects. Subjects breathed through a mouth piece connected to a pneumotachograph (Hans Ruludolph), 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 (e.g., Fig. 1B).

The method for recording neural drive to the parasternal intercostal muscles has been described previously (e.g., Gandevia et al. 1999, 2006). Briefly, the medial portions of the muscles in the second and fourth interspaces on the right side (i.e., an “upper” and “lower” interspace), ~1–2 cm lateral from the sternal edge, were located by palpation in each subject. The potential recording sites were then evaluated with a 5-MHz ultrasound linear probe (Acuson 128 XP, Acuson, Mountain View, CA). The depth of the internal edge of the parasternal intercostal relative to the skin surface ranged between 18.5 and 28.0 mm in the second interspace and between 25.0 and 45.0 mm in the fourth interspace. A topical anesthetic (Emla cream 5%) was then applied to the area of skin marked for electrode insertion for ~15 min, and in two subjects, a small dose of local anesthetic (~1 ml; lignocaine, 1%) was also injected under the skin.

Recordings were made using a Teflon-coated monopolar electrode (Medelec DMG50, Surrey, UK). The recordings were referenced to a surface electrode positioned 2–3 cm away, and the electromyographic (EMG) signal was amplified and band-pass filtered <53 Hz and >3,000 Hz. Because the recording depths had been examined by ultrasonography, we could define the maximal possible length of the needle track and mark this on the electrode. The needle was inserted perpendicular to the skin surface and advanced in small steps into the parasternal intercostal. EMG activity was continuously monitored on a loudspeaker and an oscilloscope throughout the procedure, and once a site in the parasternal intercostal was encountered that contained single motor-unit activity with an acceptable signal-to-noise ratio (>3:1) during quiet breathing or mild voluntary hyperpnoea, the audio signal was removed. After completion of the experimental protocol (see following text), the needle was moved to a different site within the muscle. In each subject, 3–10 sites were studied in both the second and the fourth interspace. In two subjects, there was little inspiratory activity in the fourth interspace, so the third interspace was studied instead.

All signals were stored on computer via a Cambridge Electronic Design 1401 interface (Cambridge, UK) for subsequent analysis. EMG was sampled at 10 kHz, and airflow, volume, and force at 1 kHz.

**Experimental protocol**

Parasternal 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 their hips. Then under instruction from an experimenter, the subject remained apnoeic for a few seconds at end expiration and made an isometric rotation effort of the thorax about the vertical axis in either the right or the left direction. Thus to rotate to the right, the subject made an isometric contraction against the load cell below the left clavicle (e.g., Fig. 1B), 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 referred to as “rotations” in the remainder of the manuscript. Subjects were specifically instructed to keep the pectoralis muscles quiescent during rotations. After the rotation was achieved, the subject resumed quiet breathing for 20–30 s while maintaining a constant rotational force. The subject then relaxed back to the neutral position. For the six subjects, a total of 120 ipsilateral rotation efforts and 123 contralateral rotation efforts were recorded.

**Data analysis**

For each rotation, three breaths recorded in the neutral posture immediately before the rotation (“neutral breaths”), the period of apnoea during which the rotation was performed, and three breaths recorded with trunk rotated (“rotated breaths”) were analyzed. As recordings were made from parasternal intercostal muscles on the right side, rotations to the right represent ipsilateral rotations, and rotations to the left represent contralateral rotations. Analysis was made in two stages.

First, multiunit EMG activity from all periods of breathing (corresponding to different recording sites in the muscle) was digitally integrated off-line with a leaky integrator (decay time constant, 100 ms), and the peak integrated signal during inspiration was measured, relative to the signal during the last third of expiration, for neutral
breathe 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 the preceding neutral breaths. The proportion of inspiratory time that the muscles were active in the neutral and rotated breaths was also measured in these breaths. Thus for each breath, inspiratory time ($T_i$) was measured from the airflow signal, and the time of onset ($T_o$) of the integrated EMG signal was determined relative to the onset of inspiratory flow to give ($T_i - T_o$) and, with it ($T_i - T_o$)/$T_i$. Measurements of tidal volume, mean inspiratory flow, and isometric rotational force during these breaths were also made. Force was measured from the load cell at which the compression force was made, i.e., at the left load cell for ipsilateral rotations, and at the right load cell for contralateral rotations.

The second stage of analysis examined the behavior of single motor units. This technique has been described previously in detail (Gandevia et al. 1999, 2006). The neutral and rotated breaths that were considered for the multunit analysis as well as the apnoeic period of rotation were analyzed using a commercial software package (Spike 2; Cambridge Electronic Design, Cambridge, UK). Trigger levels were set manually to capture all spikes with an appropriate signal-to-noise ratio. They were subsequently recalled and manually sorted into “templates” based on their size and detailed morphology. The interactive software allowed: updating of the mean shape of the template for each motor unit, review of the frequency plots of each single motor unit together with inspiratory flow and lung volume, and superimposition of all spikes from a particular motor unit (e.g., Fig. 3). Using this method, we could follow simultaneously the discharge of up to four single motor units over several consecutive breaths and isometric rotation of the thorax. For each unit, the peak discharge frequency was measured during inspiration, and for units with background tonic activity, the tonic discharge rate was measured from the plateau in the last third of expiration. The discharge frequency of motor units active during the rotation (e.g., unit 1 in Fig. 3A) was also measured.

Most motor units discharged in both neutral breaths and rotated breaths, so the respiratory-related activity could be compared directly. However, for ipsilateral rotations, some motor units discharged in the rotated breaths that were not active in the preceding neutral breaths. Such units were considered in the data analysis only if one could ensure that the position of the needle was maintained throughout the rotation, i.e., if one or two motor units were active in both sets of breaths and if the motor units that were active in the neutral breaths before the rotation were still recorded following the return to the neutral position. On the other hand, if we could not confirm that the position of the needle had been maintained with the change in posture, the units were omitted from the analysis altogether. Conversely, for contralateral rotations, some units that were active in neutral breaths were no longer found in the rotated breaths. Again these units were included in the analysis only if the position of the needle was shown to be maintained.

For each recording site, respiratory variables, isometric compression force, peak inspiratory EMG activity, ($T_i - T_o$)/$T_i$, and discharge rates for single motor units were averaged over the three neutral breaths and over the three rotated breaths recorded from that site. For the respiratory and multunit data, values obtained were then averaged over all sites for each subject, and they were then averaged for the upper (second) interspace and lower (third or fourth) interspace. As the values of peak EMG activity and ($T_i - T_o$)/$T_i$ were similar in recordings from the upper and lower interspaces for ipsi- and contralateral rotations ($P = 0.1$ for both), these values, as well as the respiratory variables, were averaged over the two interspaces.

Single motor units with respiratory-related activity were classified as “phasic” or “tonic” for each rotation. By convention, phasic units were active only during inspiration and had no background tonic activity, whereas tonic units had inspiratory modulation of tonic activity in either neutral breaths, rotated breaths, or both. Because the specific objective of this study was to assess the behavior of the parasternal intercostals during rotation of the trunk, we focused on those motor units that could be measured reliably in both neutral and rotated breaths. In a previous study when we assessed neural drive to the first to fifth parasternal intercostal muscles, we found a rostral-caudal gradient of neural drive, but there were not always statistically significant differences in discharge rate between all interspaces (Gandevia et al. 2006). In the current study, there was no statistical difference in the discharge rate of units from the second and fourth spaces. Therefore single motor-unit data were also averaged across interspaces.

### Statistics

Group data are presented as means ± SE. Student’s paired $t$-test was used to compare respiratory variables, force, peak integrated EMG activity, and ($T_i - T_o$)/$T_i$ between neutral breaths and rotated breaths. Statistical comparisons between the discharge rates of motor units in the different parasternal interspaces were made by ANOVA or by Kruskal-Wallis ANOVA on ranks for nonparametric data. Comparison of the discharge rate of motor units that were active in both neutral and rotated breaths was made using Student’s paired $t$-test or by Mann Whitney rank sum test. The number of units with background tonic activity in ipsi- and contralateral rotations was compared using a $\chi^2$ analysis. The criterion for statistical significance was taken as $P < 0.05$.

### RESULTS

Representative recordings obtained during ipsilateral and contralateral rotation of the trunk in one subject are shown in Fig. 2. For the six subjects, the rotary force developed in ipsilateral rotation efforts averaged 2.2 ± 0.2 Nm (range, 0.3–4.2 Nm) and the force developed in contralateral rotation was 1.7 ± 0.2 Nm (range, 0.2–4.1 Nm; $P < 0.001$). However, whereas the parasternal intercostals were usually active during the apnoeic period of ipsilateral rotation, they were invariably silent during the apnoeic period of contralateral rotation. In addition, rotations were associated with marked alterations in inspiratory activity.

#### Inspiratory activity in rotated postures

The indices of the pattern of breathing during neutral breaths and rotated breaths are summarized in Table 1. For both ipsilateral and contralateral rotations, tidal volume and inspiratory time were slightly but significantly smaller during rotated breaths than during neutral breaths ($P < 0.05$ or less).

In all subjects, the parasternal intercostals showed phasic inspiratory activity in both neutral and rotated breaths. However, the peak inspiratory activity in rotated breaths was consistently different from that in neutral breaths, and inspiratory activity during ipsilateral rotation was consistently different from that during contralateral rotation. Thus for the 12 interspaces investigated in the six subjects, the peak parasternal inspiratory activity during ipsilateral rotation was 201 ± 19% of the peak activity in neutral breaths ($P < 0.001$), whereas during contralateral rotation, it was only 72 ± 4% of the peak activity in neutral breaths ($P < 0.001$).

The timing of inspiratory activity was also altered by rotation. Activity during ipsilateral rotation appeared earlier, relative to the onset of inspiratory airflow, than in neutral breaths. As a result, whereas the duration of inspiratory activity ($[T_i - T_o]/T_i$) was 84.5 ± 3.7% in neutral breaths, it was 99.0 ± 1.4% during ipsilateral rotation ($P < 0.001$). On the other hand, during contralateral rotation, the onset of inspiratory activity was...
Inspiratory single motor-unit activity in rotated postures

Typical examples of motor-unit activity in the parasternal intercostals during breathing in the neutral posture, during ipsilateral or contralateral rotation of the trunk, and during breathing with the trunk rotated are shown for one subject in Fig. 3. The vast majority of the 354 single motor units discriminated from in the second, third, and fourth interspaces discharged in phase with inspiration. Of these units, 321 (~91%) were active exclusively during inspiration, and 29 (~8%) had inspiratory modulation of tonic activity in either neutral breaths or rotated breaths or both. Thus only 4/354 units (1%) did not have discharge patterns related to the respiratory cycle (see following text).

During ipsilateral rotation (Figs. 3A and 4A), the peak inspiratory discharge frequency of the phasic units that were active in both neutral breaths and rotated breaths (n = 81) increased from 11.0 ± 0.3 Hz in neutral breaths to 14.3 ± 0.3 Hz in rotated breaths (P < 0.001). Also although one motor unit that was active in neutral breaths no longer discharged in rotated breaths, 68 units that were not active in neutral breaths were active in rotated breaths. These new units discharged at 12.9 ± 0.3 Hz. In contrast, during contralateral rotation (Figs. 3B and 4B), the inspiratory discharge frequency of the phasic units that were active in both neutral and rotated breaths (n = 118) decreased from 12.0 ± 0.2 Hz in neutral breaths to 10.5 ± 0.2 Hz in rotated breaths (P < 0.001), and 54 units that discharged in neutral breaths with an average frequency of 10.7 ± 0.3 Hz were no longer active. After rotations, the same motor units discharged in the subsequent neutral breaths.

A larger number of units also discharged tonically in breathing during ipsilateral rotation (n = 21) than in breathing during contralateral rotation (n = 3; P < 0.001). As shown in Fig. 5, the units that discharged with inspiratory modulation of tonic activity during ipsilateral rotation were either active in neutral breaths with phasic activity only (n = 15; e.g., Fig. 5A) or did not discharge at all in neutral breaths (n = 6; Fig. 5B). The three motor units with inspiratory modulation of tonic activity during contralateral rotation were already active in the preceding neutral breaths and also had inspiratory modulation of tonic activity (Fig. 5B).

Single motor-unit activity during rotation

Figures 3A and 5A show typical examples of motor-unit activity in the parasternal intercostals during the initial, apneic period of ipsilateral rotation. During this period, activity was observed in 65 units (~44%, 65/149 units), and their discharge frequency was 10.2 ± 0.4 Hz. The vast majority of these motor units (n = 61) had definite respiratory modulation in the subsequent rotated breaths. The remaining units were either silent during breathing (n = 2) or exhibited tonic activity only (n = 2). In contrast, no single motor-unit activity was delayed, such that (T1 - T0)/T1 was reduced from 89.2 ± 3.5% in neutral breaths to 78.8 ± 4.8% in rotated breaths (P < 0.01).

Inspiratory single motor-unit activity in rotated postures

Typical examples of motor-unit activity in the parasternal intercostals during breathing in the neutral posture, during ipsilateral or contralateral rotation of the trunk, and during breathing with the trunk rotated are shown for one subject in Fig. 3. The vast majority of the 354 single motor units discriminated from in the second, third, and fourth interspaces discharged in phase with inspiration. Of these units, 321 (~91%) were active exclusively during inspiration, and 29 (~8%) had inspiratory modulation of tonic activity in either neutral breaths or rotated breaths or both. Thus only 4/354 units (1%) did not have discharge patterns related to the respiratory cycle (see following text).

During ipsilateral rotation (Figs. 3A and 4A), the peak inspiratory discharge frequency of the phasic units that were active in both neutral breaths and rotated breaths (n = 81) increased from 11.0 ± 0.3 Hz in neutral breaths to 14.3 ± 0.3 Hz in rotated breaths (P < 0.001). Also although one motor unit that was active in neutral breaths no longer discharged in rotated breaths, 68 units that were not active in neutral breaths were active in rotated breaths. These new units discharged at 12.9 ± 0.3 Hz. In contrast, during contralateral rotation (Figs. 3B and 4B), the inspiratory discharge frequency of the phasic units that were active in both neutral and rotated breaths (n = 118) decreased from 12.0 ± 0.2 Hz in neutral breaths to 10.5 ± 0.2 Hz in rotated breaths (P < 0.001), and 54 units that discharged in neutral breaths with an average frequency of 10.7 ± 0.3 Hz were no longer active. After rotations, the same motor units discharged in the subsequent neutral breaths.

A larger number of units also discharged tonically in breathing during ipsilateral rotation (n = 21) than in breathing during contralateral rotation (n = 3; P < 0.001). As shown in Fig. 5, the units that discharged with inspiratory modulation of tonic activity during ipsilateral rotation were either active in neutral breaths with phasic activity only (n = 15; e.g., Fig. 5A) or did not discharge at all in neutral breaths (n = 6; Fig. 5B). The three motor units with inspiratory modulation of tonic activity during contralateral rotation were already active in the preceding neutral breaths and also had inspiratory modulation of tonic activity (Fig. 5B).

Single motor-unit activity during rotation

Figures 3A and 5A show typical examples of motor-unit activity in the parasternal intercostals during the initial, apneic period of ipsilateral rotation. During this period, activity was observed in 65 units (~44%, 65/149 units), and their discharge frequency was 10.2 ± 0.4 Hz. The vast majority of these motor units (n = 61) had definite respiratory modulation in the subsequent rotated breaths. The remaining units were either silent during breathing (n = 2) or exhibited tonic activity only (n = 2). In contrast, no single motor-unit activity was delayed, such that (T1 - T0)/T1 was reduced from 89.2 ± 3.5% in neutral breaths to 78.8 ± 4.8% in rotated breaths (P < 0.01).

Inspiratory single motor-unit activity in rotated postures

Typical examples of motor-unit activity in the parasternal intercostals during breathing in the neutral posture, during ipsilateral or contralateral rotation of the trunk, and during breathing with the trunk rotated are shown for one subject in Fig. 3. The vast majority of the 354 single motor units discriminated from in the second, third, and fourth interspaces discharged in phase with inspiration. Of these units, 321 (~91%) were active exclusively during inspiration, and 29 (~8%) had inspiratory modulation of tonic activity in either neutral breaths or rotated breaths or both. Thus only 4/354 units (1%) did not have discharge patterns related to the respiratory cycle (see following text).

During ipsilateral rotation (Figs. 3A and 4A), the peak inspiratory discharge frequency of the phasic units that were active in both neutral breaths and rotated breaths (n = 81) increased from 11.0 ± 0.3 Hz in neutral breaths to 14.3 ± 0.3 Hz in rotated breaths (P < 0.001). Also although one motor unit that was active in neutral breaths no longer discharged in rotated breaths, 68 units that were not active in neutral breaths were active in rotated breaths. These new units discharged at 12.9 ± 0.3 Hz. In contrast, during contralateral rotation (Figs. 3B and 4B), the inspiratory discharge frequency of the phasic units that were active in both neutral and rotated breaths (n = 118) decreased from 12.0 ± 0.2 Hz in neutral breaths to 10.5 ± 0.2 Hz in rotated breaths (P < 0.001), and 54 units that discharged in neutral breaths with an average frequency of 10.7 ± 0.3 Hz were no longer active. After rotations, the same motor units discharged in the subsequent neutral breaths.

A larger number of units also discharged tonically in breathing during ipsilateral rotation (n = 21) than in breathing during contralateral rotation (n = 3; P < 0.001). As shown in Fig. 5, the units that discharged with inspiratory modulation of tonic activity during ipsilateral rotation were either active in neutral breaths with phasic activity only (n = 15; e.g., Fig. 5A) or did not discharge at all in neutral breaths (n = 6; Fig. 5B). The three motor units with inspiratory modulation of tonic activity during contralateral rotation were already active in the preceding neutral breaths and also had inspiratory modulation of tonic activity (Fig. 5B).

Values are means ± SE for six subjects during quiet breathing in a neutral posture and quiet breathing while ipsilateral or contralateral rotation of the thorax was maintained. Tidal volume (Vt), inspiratory time (Ti), mean inspiratory flow (Vt/Ti), and the isometric force of the rotations are shown. *Significantly different from recordings in neutral breaths (for ipsilateral rotations: P < 0.01 for Vt and Vt/Ti; for contralateral rotations: P < 0.05 for Vt, P < 0.001 for Vt/Ti). †Significantly different from ipsilateral rotations (P < 0.01).

J Neurophysiol • VOL 103 • MARCH 2010 • www.jn.org
recorded during the apnoeic period of contralateral rotation (Fig. 3B).

**DISCUSSION**

The fibers of the parasternal intercostal muscle in a given interspace run caudally and laterally from the costal cartilage above to the costal cartilage below. Based on this orientation, we predicted that although the mass of these muscles in humans is small (De Troyer et al. 1998), their contraction in all interspaces on one side of the sternum would induce a lateral and backward displacement of the uppermost ribs relative to the lower ribs. The present measurements confirmed, in agreement with the hypothesis, that the parasternal intercostals on the right side contract during rotation of the trunk to the right but remain silent during rotation of the trunk to the left. In addition, we established that most of the motor units that are active during rotation of the trunk also discharge in the inspiratory phase of the breathing cycle. Finally, and more importantly, we also showed that the involvement of the parasternal intercostals in rotations of the trunk causes alterations in the activation of the muscles during inspiration in a direction-dependent manner. This observation has important implications for the integration of postural and inspiratory drive.

**Parasternal inspiratory activity with ipsilateral rotation**

Breathing during ipsilateral rotation of the trunk was associated with a small reduction in tidal volume ($V_T$) and inspiratory time ($T_I$) without any change in mean inspiratory flow ($V_{TI}$; Table 1). This suggests that during such rotation, the inspiratory output to the parasternal (and presumably other inspiratory) muscles was unaltered but terminated a little earlier, so it would be expected that peak parasternal inspiratory activity and $(T_I - T_{0I})/T_I$ would decrease slightly. Instead peak inspiratory activity in the parasternal intercostals increased substantially with every ipsilateral rotation (due to the recruitment of new motor units and an increase in peak discharge frequency of the units that were already active during breathing in the neutral posture), and activity consistently appeared earlier relative to the onset of inspiratory flow. It is also notable that the increase in discharge frequency of the parasternal motor units in inspiration during ipsilateral rotation of the trunk was...
larger than that observed during CO₂-induced hyperpnoea. This increase was 1.9 Hz when ventilation increased threefold (Gandevia et al. 1999), whereas during ipsilateral rotation, the increase was 3.3 Hz. Therefore with rotation of the trunk, the output of the ipsilateral parasternal motoneurons during inspiration is greatly increased.

This increase in inspiratory output is presumably related to activity in descending pathways that arise from the motor cortex (Gandevia and Plassman 1988; Gandevia and Rothwell 1987) and the medulla (e.g., Davies et al. 1985; Duffin and Lipski 1987; Hilaire and Monteau 1976; Merrill and Lipski 1987). The combination of postural and inspiratory drives would effectively decrease the threshold of motoneurons during inspiration such that the output of motoneurons is increased. However, it is also possible that during rotation of the trunk to the right, tonic contraction of the parasternal intercostals and internal interosseous intercostals (Whitelaw et al. 1992) on the right side induces a decrease in the compliance of the right half of the rib cage. As a result, the load applied to the parasternal intercostals during inspiration would be greater, leading to an increase in the afferent input from muscle spindles which would increase motoneuron output. The parasternal intercostals in the cat are known to contain very few muscle spindles (Duron et al. 1978), and EMG recordings from these muscles in anesthetized dogs have shown that inspiratory activity does not increase when external loads are applied to the ribs (De Troyer 1996) or when high-frequency mechanical vibration is applied to the chest (Leduc et al. 2000). However, in humans, cortical potentials and spinal reflexes can be recorded in response to low-threshold microstimulation or a mechanical "tap" applied to the parasternal intercostals (Gandevia and Macefield 1989; Macefield and Gandevia 1992), suggesting that, in humans, these muscles do contain muscle spindles (see also Butler et al. 1997).

Parasternal inspiratory activity with contralateral rotation

In contrast to ipsilateral rotation, contralateral rotation of the trunk elicited a decrease in the peak inspiratory activity of the parasternal intercostals and in the proportion of inspiratory time that the muscles were active. This decrease might be related in part to the decrease in \( V_T \) and \( T_I \). However, the changes in \( V_T \) and \( T_I \) were small, only 6% of the values recorded in neutral breaths (Table 1). In addition, analysis of single motor-unit activity showed that a number of motor units that were active in neutral breaths stopped firing during contralateral rotation and that the motor units that were active during inspiration in the two postures usually discharged with lower firing rates during rotation. Such alterations cannot be accounted for on the basis of a small decrease in \( V_T \) and \( T_I \). Rather they imply that the motoneuronal output during inspiration was actually diminished.

In limb muscles, during contraction of an agonist, there is reciprocal inhibition of antagonist muscles to reduce disadvantageous co-contraction (Nielsen et al. 1995; for review, see Crone and Nielsen 1994; Pierrot-Deseilligny and Burke 2005). In the respiratory system, there is reciprocal inhibition between the inspiratory and expiratory intercostal muscles during breathing (Andersen and Sears 1970; Sears 1964). Similarly, we speculate that during rotation of the trunk, there is reciprocal inhibition between the parasternal intercostals and the triangularis sterni in the ventral portion of the rib cage. The fibers of the triangularis sterni run cranially and laterally from the dorsal aspect of the sternum to the lateral portion of the costal cartilages. Thus the fibers of the triangularis sterni on the right are expected to contract during rotation of the trunk to the left, and they do (Kobayashi et al. 2003). The far-field activity observed during the apnoeic period of contralateral rotation in Fig. 3B supports this idea. Through reciprocal inhibition, such a contraction of the triangu-

**Fig. 4.** Inspiratory discharge frequency of motor units active in neutral breaths and rotated breaths. Data from recordings in the 2nd, 3rd, and 4th parasternal intercostal muscles from 6 subjects. The inspiratory discharge rate of units active in neutral breaths is plotted against their inspiratory rate in rotated breaths during ipsilateral rotation (A) or during contralateral rotation (B). ○, units that were active in both neutral and rotated breaths; □, units that were recruited in rotated breaths during ipsilateral rotation and units that were derecruited in rotated breaths during contralateral rotation; ● and ■, means ± SE. During ipsilateral rotation (A), in addition to an increase in the discharge rate of motor units active in both neutral and rotated breaths (\( n = 81 \) units), 68 new motor units discharged in phase with inspiration; only 1 unit that discharged in neutral breaths was no longer active. In contrast, during contralateral rotation (B), the discharge rate was less than in neutral breaths (\( n = 118 \) units), and 54 units that were active in neutral breaths were no longer active. Units with tonic activity were omitted from this figure (see Fig. 5).
An additional possibility is that there may be crossed reciprocal inhibition between the parasternal intercostal muscles on both sides of the thorax. Stretch reflexes can be evoked in some human axial muscles contralateral to a ‘‘muscle tap’’ (Alexander and Harrison 2002; Beith and Harrison 2004), which suggests that contralateral motoneurons can be influenced by reflexes originating on the ipsilateral side.

Integration of postural and respiratory drive

Neurons in the pontomedullary reticular formation are important for postural maintenance, for example, to ensure an upright posture in locomotion or reaching (for review, see Drew et al. 2004). Although these neurons can affect respiratory muscle activity, for example in postural alterations that activate the vestibular system (Mori et al. 2001), in the current study, we use the term postural command to mean a voluntary command for trunk rotation. Postural and respiratory commands act on the same parasternal intercostal motoneurons, but where are these commands integrated? When the parasternal intercostal muscles are involved in trunk rotation, postural command from the motor cortex may act at the medulla and alter the inspiratory bulbospinal output to the motoneurons on different sides of the sternum with an increase in inspiratory drive to motoneurons on one side, but a decrease in drive to the other side. However, although descending drive from the motor cortex can alter medullary neuron output (Bassal et al. 1981; Orem 1989; Orem and Netick 1986), connections that excite inspiratory bulbospinal neurons have not yet been demonstrated.

Alternatively, premotor drive from multiple descending pathways, i.e., from the motor cortex for postural functions and from the medulla for respiratory function, may be integrated at the spinal cord (e.g., Aminoff and Sears 1971; Bellingham 1999). Bilateral projections from inspiratory medullary neurons to intercostal and phrenic motoneurons have been revealed in several species using anterograde and retrograde tracers (e.g., Dobbins and Feldman 1994; Ellenberger et al. 1990; Feldman et al. 1985; Lipski et al. 1994; Rikard-Bell et al. 1984, 1985; Yamada et al. 1988), and electrophysiological studies (Duffin and van Alphen 1995; Hoskin and Duffin 1987; Lipski et al. 1994; Tian and Duffin 1996). We posit that there is strong bilateral control of the respiratory muscles via bulbospinal pathways for respiration and that inspiratory drive to both sides of the thorax is coupled and quantitatively similar. Therefore the direction-dependent effects of trunk rotation on inspiratory drive would come about because of the change in input to the parasternal intercostal motoneurons. This may be due to direct, oligosynaptic pathways from the human motor cortex to the intercostal motoneurons (Gandevia and Plasmann 1988) as well as local spinal reflexes (see preceding text). At the spinal cord, all inputs acting on motoneurons and interneurons including spinal reflexes can be coordinated to produce the appropriate motor unit output (see Bellingham 1999). The mechanism that generates the rostrocaudal gradient of parasternal intercostal motoneuron output in both voluntary and involuntary breaths is also likely to occur at the spinal cord rather than in the medulla (Hudson et al. 2008; see also DiMarco and Kowalski 2009; Kowalski and DiMarco 2009).

In different motor tasks associated with limb movement, common motoneurons are employed, but their functional output is quite different (e.g., Soffe 1993). This also appears to be the case for the human parasternal intercostal motor units and their output in inspiratory and postural tasks. Changes in the output of parasternal intercostal motoneurons during a combined postural and inspiratory task reveal the interplay between the multiple descending drives to these motoneurons, and we propose that these premotor drives are integrated at the level of both spinal interneurons and motoneurons.

G R A N T S

This work was supported by grants from the National Health and Medical Research Council.
BREATHING WITH A TWIST

1629

REFERENCES


