Postinspiratory activity of the parasternal and external intercostal muscles in awake canines

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Easton, Paul A., Harvey G. Hawes, Bruce Rothwell, and Andre De Troyer. Postinspiratory activity of the parasternal and external intercostal muscles in awake canines. J. Appl. Physiol. 87(3): 1097–1101, 1999.—Previous studies have shown in awake dogs that activity in the crural diaphragm, but not in the costal diaphragm, usually persists after the end of inspiratory airflow. It has been suggested that this difference in postinspiratory activity results from greater muscle spindle content in the crural diaphragm. To evaluate the relationship between muscle spindles and postinspiratory activity, we have studied the pattern of activation of the parasternal and external intercostal muscles in the second to fourth interspaces in eight chronically implanted animals. Recordings were made on 2 or 3 successive days with the animals breathing quietly in the lateral decubitus position. The two muscles discharged in phase with inspiration, but parasternal intercostal activity usually terminated with the cessation of inspiratory flow, whereas external intercostal activity persisted for 24.7 ± 12.3% of inspiratory time (P < 0.05). Forelimb elevation in six animals did not affect postinspiratory activity in the parasternal but prolonged postinspiratory activity in the external intercostal to 45.4 ± 16.3% of inspiratory time (P < 0.05); in two animals, activity was still present at the onset of the next inspiratory burst. These observations support the concept that muscle spindles are an important determinant of postinspiratory activity. The absence of such activity in the parasternal intercostals and costal diaphragm also suggests that the mechanical impact of postinspiratory activity on the respiratory system is smaller than conventionally thought.

inspiratory intercostals; muscle spindles; body position; chest wall mechanics

ELECTROMYOGRAPHIC (EMG) recordings from the diaphragm in awake dogs have shown a clear difference in the pattern of activity between the crural and costal portions of the muscle. Specifically, activity of the crural portion persists well after the end of inspiratory flow, whereas activity of the costal portion terminates with the cessation of inspiratory flow (10). This regional difference in postinspiratory activity was recorded both during rest with room-air breathing and during hyperpnea induced by CO₂ or hypoxia; in fact, the regional difference was greater during hyperpnea than during room air breathing (10, 11). Although the mechanism of this difference was not identified, it was suggested that the greater postinspiratory activity of the crural dia-

phragm was related to the greater spindle content of the muscle (10, 11).

To test the idea that muscle spindles are an important determinant of postinspiratory activity, we have assessed in awake, intact canines the pattern of activation of the two predominant groups of inspiratory intercostal muscles, namely, the parasternal intercostals and the external intercostals in the rostral intercostal spaces. Indeed, histological studies have shown in the cat that the external intercostals in the rostral intercostal spaces contain much larger numbers of muscle spindles than do the parasternal intercostals (8), and this difference is known to play a major role in determining the response of these muscles to increases in inspiratory mechanical load. When the inspiratory airflow resistance is suddenly increased in anesthetized cats (1, 23), rabbits (20), and dogs (3) or when the airway is occluded at end expiration for a single breath (2), the external intercostals in the rostral intercostal spaces show an increased rate of rise of activity. This facilitation of activity is associated with an increased spindle afferent activity (1) and is eliminated by section of the thoracic dorsal roots (1, 2, 20). In contrast, increases in inspiratory airflow resistance or single-breath airway occlusion in anesthetized dogs causes little alteration in parasternal intercostal activity (2, 3). Similarly, when an external force is applied to the ribs to reduce their normal inspiratory cranial displacement, there is a reflex, spindle-induced increase in external intercostal inspiratory activity without any alteration in parasternal intercostal activity (4, 16). Therefore, if spindle density were a significant determinant of the presence or absence of postinspiratory activity, the external intercostals should show greater postinspiratory activity than should the parasternal intercostals.

METHODS

The project was approved by the Animal Care Committee at the University of Calgary. Eight adult mongrel canines (mean weight 27.3 kg; range 20–33 kg) were familiarized with the laboratory environment and personnel and were trained over several weeks to breathe quietly in different body positions. After this period of training, bipolar fine-wire EMG electrodes were implanted in the parasternal intercostal and external intercostal muscles of the second to fourth left intercostal spaces. This technique of EMG implantation has been described in detail elsewhere (10, 14, 18). Briefly, with the animals under general anesthesia, the skin was incised and deflected over the sternum, and bipolar EMG wires were implanted in the parasternal intercostal muscle of the second, third, or fourth intercostal space, ~1–2 cm lateral to the edge of the sternum. The external intercostals were exposed by a second incision on the lateral chest wall, and a pair of EMG

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wires was implanted in the midaxillary line; the two wires of each pair were placed ~1 cm apart along the long axis of a muscle bundle. The implants were secured by fine, synthetic, nonfibrogenic sutures (Prolene, Ethicon); wires were externalized; and the animals were allowed to recover. There was no operative or postoperative complication. The canines were awake and ambulatory within 3–6 h of the operation and were freely active and feeding normally within 1–2 days. When the studies were completed, the animals were euthanized, and the intercostal muscles were examined. The implantation sites showed minimal fibrosis, as noted in earlier studies on the diaphragm by Easton et al. (10).

All measurements were performed with the animals awake and breathing quietly at laboratory temperature of 18–20°C. The animals breathed spontaneously through a snout mask, and breathing quietly at laboratory temperature of 18–20°C. The canines were awake and ambulatory within 3–6 h of the operation and were freely active and feeding normally within 1–2 days. When the studies were completed, the animals were euthanized, and the intercostal muscles were examined. The implantation sites showed minimal fibrosis, as noted in earlier studies on the diaphragm by Easton et al. (10).

Vertical dotted lines, onset and termination of inspiratory activity in external intercostal.

RESULTS

Breathing pattern for the eight animals studied was as follows: VT 0.32 ± 0.07 (SD) liter, respiratory rate 31 ± 10 breaths/min, VT 9.76 ± 3.4 l/min, Ti 0.94 ± 0.26 s, and VT/Ti 0.36 ± 0.1 1/s. The parasternal and external intercostal muscles were active in phase with inspiratory flow in all animals, and the onset of activity generally coincided with the onset of inspiratory flow in both muscles. For the group, parasternal intercostal activity could be recognized 2.2 ± 3.7% of Ti before the

![Image](http://jap.physiology.org/DownloadedFrom/to/10.22032.247OnOctober15,2017)
first moment of inspiratory airflow, and external intercostal activity was observed 0.6 ± 4.1% of T_I after the onset of inspiratory flow (not significant). However, whereas parasternal intercostal activity terminated simultaneously with the cessation of inspiratory airflow, external intercostal activity commonly carried on after the end of inspiratory airflow into the subsequent expiration. A striking example of this difference is shown in Fig. 1. For the animal group, the duration of postinspiratory activity in the external intercostals averaged 24.7 ± 12.3% of T_I or 10.2 ± 5.1% of T_tot; corresponding values for the parasternal intercostals were 3.9 ± 5.7% of T_I and 1.2 ± 2.5% of T_tot (P < 0.05).

This difference in postinspiratory activity between the parasternal and the external intercostal persisted when the forelimb was lifted, as shown by the recordings of a representative animal in Fig. 2. In fact, postinspiratory activity in the external intercostal was prolonged with forelimb lifting in all animals, and, in two of them, the change was so prominent that commonly activity was still present at the onset of the next inspiratory burst (Fig. 3). For the six animals, postinspiratory activity in the external intercostal in this position thus lasted for 45.4 ± 16.3% of T_I or 17.7 ± 6.5% of T_tot; these values are significantly greater than those in the resting arm position (P = 0.05). In contrast, postinspiratory activity in the parasternal intercostal remained at 4.2 ± 5.8% of T_I or 1.1 ± 2.4% of T_tot (not significant).

**DISCUSSION**

Previous studies in anesthetized dogs (3, 5, 6) and cats (13, 15, 21) have shown that the parasternal intercostal muscles and the external intercostals in the rostral interspaces discharge during the inspiratory phase of the breathing cycle, and intracellular recordings from respiratory motoneurons in the thoracic spinal cord in cats have clearly established that these rhythmic inspiratory discharges are related to centrally induced alterations in membrane potential. These alterations are usually referred to as "central respiratory drive potentials" (12, 22). Thus the parasternal and external intercostal α-motoneurons depolarize during inspiration to reach the threshold of activation and send efferent impulses to the corresponding muscles.
This depolarizing phase is then followed by a hyperpolarizing phase during expiration so that the motoneurons remain below the activation threshold and the muscles are kept silent. Because our animals had synchronous parasternal and external intercostal activity at the onset of inspiration, one may therefore conclude that the parasternal and external intercostal α-motoneurons in awake dogs depolarize simultaneously.

However, whereas the activity recorded from the parasternal intercostals ended together with inspiratory flow, external intercostal activity continued well after the cessation of inspiration. Postinspiratory activity in the external intercostals was also greater than postinspiratory activity in the parasternal intercostals when animals lifted the forelimb; in some animals external intercostal activity even persisted throughout expiration. This difference between the parasternal and external intercostals is qualitatively similar to that seen between the costal and crural portions of the diaphragm (10, 11), and this is fully consistent with our hypothesis that muscle spindles are a primary determinant of this phenomenon.

The mechanism by which muscle spindles might induce postinspiratory activity cannot be readily demonstrated at this stage but could be explained on the basis of the respiratory changes in muscle length. Studies in which sonomicrometry was used in anesthetized dogs have shown that the external intercostals in the rostral interspaces and the parasternal intercostals shorten in phase with inspiration (3, 5–7). Thus both muscles become gradually shorter as inspiration proceeds, reach their shortest length at peak inspiration, and then lengthen rather abruptly in early expiration. To the extent that muscle spindles are situated in parallel with the (extrafusal) muscle fibers, this muscle lengthening should induce stretching of the central, sensitive portion of the spindles in early expiration. Therefore, the external intercostal muscle spindles should elicit excitatory postsynaptic potentials in the corresponding α-motoneurons (22). As a result, the membrane potential of the motoneurons could be maintained above the activation threshold after the end of inspiration, such that efferent activity might be either synchronous with parasternal or external intercostals. As a result, the muscles would persist. On the other hand, because the parasternal intercostals are poorly endowed with spindles, the parasternal α-motoneurons should be little, if at all, affected by this mechanism. Consequently, efferent α-motor activity to these muscles should cease together with the central respiratory drive potential, i.e., at or near the end of inspiration.

It is traditionally considered that postinspiratory activity causes braking of expiratory airflow and plays an important role in the regulation of end-expiratory lung volume (19). Yet, previous studies of Easton et al. (10, 11) and the present observations indicate that, in awake dogs, activity in the costal diaphragm and the parasternal intercostals terminates with the cessation of inspiratory flow. Because these two sets of muscles have the greatest inspiratory effect in the dog, one may question the functional significance of postinspiratory activity. Furthermore, recent studies in anesthetized dogs have suggested that muscle spindles in the external intercostals have relatively little impact on the mechanical behavior of the respiratory system. Although a high inspiratory-airflow resistance or a singlebreath airway occlusion at end expiration induces, through the increased spindle afferent activity, a marked increase in external intercostal inspiratory activity (2, 3), the normal inspiratory cranial displacement of the ribs is usually reversed into an inspiratory caudal displacement and the normal inspiratory muscle shortening is reversed into an inspiratory muscle lengthening (3). Similarly, when weights are attached to the ribs caudally, the cranial rib displacement and intercostal muscle shortening during inspiration are reduced, and this also leads to a reflex, spindle-induced excitation of the external intercostals; yet, denervation of the external intercostals alters the inspiratory rib displacement only moderately (16). Therefore, to the extent that postinspiratory activity would also result from a spindle mechanism, it might be envisaged as an electrical characteristic of spindle-rich inspiratory muscles without any significant mechanical effect during normal, resting breathing.

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