

THE LABILE RESPIRATORY ACTIVITY OF RIBCAGE MUSCLES OF THE RAT DURING SLEEP

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SUMMARY

1. Sleep–waking states of chronically implanted rats were identified polygraphically while recording the integrated electromyogram (e.m.g.) of extrinsic (scalenus medius and levator costae) and intrinsic (external and internal interosseous intercostal and parasternal) muscles of the thoracic cage. Rats breathed air, air enriched in CO₂ (5%) or air deficient in O₂ (10% O₂ in N₂) and were free to adopt any desired posture.

2. In non-rapid eye movement (non-r.e.m.) sleep, the scalenus medius and intercostal muscles of the cephalic spaces were always inspiratory; intercostal muscles of the mid-thoracic spaces were commonly expiratory while the more caudal ones were only occasionally expiratory. Expiratory activity, when present in quiet wakefulness, extended for a variable period of time into non-r.e.m. sleep and always disappeared in r.e.m. sleep regardless of the ribcage muscle under study.

3. Inspiratory activity, when present in non-r.e.m. sleep, was unaffected, partially attenuated or abolished at entry into r.e.m. sleep. The peak integrated e.m.g. activity of ribcage muscles was measured as a function of posture, gas mixture breathed and ribcage site: (a) the greater the degree of curled-up posture, the greater the respiratory activity of scalenus medius, an effect augmented by CO₂ but depressed by hypoxia, and (b) the more caudally placed ribcage muscles exhibited respiratory activity which was essentially unaffected by posture and gas mixture inspired.

4. The presence or absence of tonic activity in ribcage respiratory muscles during non-r.e.m. sleep was unrelated to posture. When tonic activity was present, it always disappeared in r.e.m. sleep. When expiratory activity was present in non-r.e.m. sleep, it too always disappeared in r.e.m. sleep. Inspiratory activity present in non-r.e.m. sleep was variably affected at entry into r.e.m. sleep; it was unchanged, partially attenuated or abolished.

5. It is concluded that thoracic cage muscles exhibit marked variability in their respiratory activity depending on posture, sleep–waking states and gas mixture breathed. It is postulated that the presence of tonic and/or expiratory activity in ribcage muscles during non-r.e.m. sleep reflects an increase in functional residual capacity (F.R.C.).

INTRODUCTION

The respiratory activity recorded from the thoracic musculature or its nerve supply has been the subject of intense and detailed investigation (Taylor, 1960; Sears, 1964; Corda, Euler & Lennerstrand, 1966; Remmers, 1970; Parmeggiani & Sabattini, 1972; Tusiewicz, Moldofsky, Bryan & Bryan, 1977; Duron & Marlot, 1980; Hilaire, Nicholls & Sears, 1983; Le Bars & Duron, 1984; Dick, Parmeggiani & Orem, 1984; Goldman, Loh & Sears, 1985; De Troyer, Kelly, Macklem & Zin, 1985; Goldman, Loh & Sears, 1985). However, one electromyographic study of the respiratory patterns in the unanaesthetized rabbit appears to have been overlooked. Boyd (1967, 1969) reported that rabbits carrying chronically implanted e.m.g. electrodes placed over wide areas of the thoracic cage exhibit inspiratory activity in both internal and external intercostal muscles. He also found that expiratory activity could be recorded from these same general areas in both internal and external intercostal muscles. His findings confirmed the earlier experiments of Bronk & Ferguson (1935), who demonstrated that inspiratory activity sometimes occurred in the nerve fibres supplying the external and internal intercostal muscles. The work of De Troyer *et al.* (1985) also suggests that interosseous intercostal muscles have a unified function; namely, to expand or contract the ribcage depending on lung volume. These observations throw considerable doubt on the generally accepted idea that the respective intercostal muscles are reciprocally organized, as in limb muscles.

Muscles concerned with respiratory movement of the thoracic cage can be classified as extrinsic or intrinsic. Extrinsic muscles are those which have their origins outside the thoracic cage but are inserted into the ribs, e.g. the scalene muscles, abdominal wall muscles, strap muscles and the levator costae. Intrinsic muscles have both their origins and insertions in the ribcage, e.g. intercostal muscles whether they are interosseous or interchondral. Using this terminology the diaphragm would be the only muscle classified as mixed, intrinsic and extrinsic.

We elected to systematically investigate the muscle system of the thoracic cage of the rat during sleep as the animal breathed selected gas mixtures in various body postures, a previous study having examined in detail the frequency patterns of breathing (Megirian, Ryan & Sherrey, 1980). The following extrinsic muscles were examined: scalenus medius and the caudal levator costae. The intrinsic muscles studied were the parasternal (interchondral) and interosseous intercostal muscles. This study extends our earlier findings on upper-airway respiratory muscles, which were shown to be modulated by posture, enhanced by CO₂ breathing but depressed during the breathing of an O₂-deficient gas mixture during non-rapid eye movement (non-r.e.m.) sleep (Megirian, Hinrichsen & Sherrey, 1985; Sherrey, Pollard & Megirian, 1986).

METHODS

Adult hooded rats of the Wistar strain (weight: 200–250 g) served as experimental subjects. They were premedicated with homatropine hydrobromide (Evans Medical Supplies, 30 mg/kg s.c.) and then anaesthetized with sodium pentobarbitone (Sigma, 35–40 mg/kg i.p.). One-third of the dose was given as needed, to maintain surgical anaesthesia until electrode implantation was completed.

After a general survey of muscles of all rib interspaces, a special study was made of the muscles

of the 2nd, 5th, 8th and 10th interspaces. Twelve rats were used for this study, three for each interspace. A fifth group of three rats was used for the study of scalenus medius muscle. The electrodes for all muscle implants were Teflon-coated, stainless-steel wires (Medwire Corp., Mt. Vernon, NY 316 SS 3T), and the technique was that suggested by Basmajian & Stecko (1962).

In all rib interspaces mentioned above, both the internal and external intercostal muscles were implanted in the mid-axillary line. They were exposed through a longitudinal skin incision, and after the overlying muscles had been separated from their ribcage attachments. So as to avoid spurious recording of electrical activity between the two layers of muscles, the external intercostal was divided at its caudal rib attachment and rotated upwards thus exposing the underlying internal intercostal. An unambiguously different configuration of the integrated electromyograms (e.m.g.s) also confirmed that recordings had been made from separate muscles. It was unnecessary to use this technique for the 10th interspace as the external intercostal muscle is deficient anteriorly and the internal intercostal is deficient posteriorly. Thus, both muscles could be implanted without separation of the external intercostal from its caudal rib attachment. As well as the intercostal muscles, in the 2nd and 5th interspaces, the parasternal (interchondral) muscles were implanted and in the 8th and 10th interspaces electrodes were placed in the levator costae muscles.

The scalenus anterior muscle is absent in the rat and the scalenus medius is inserted into the upper six ribs. The approach to the scalenus medius muscle was through a mid-clavicular longitudinal incision and after dividing the pectoral muscles it was clearly visible.

After exposing the dorsum of the skull, gold-plated brass screws were placed in burr holes drilled into the frontal and parietal bones. A pair of fine Teflon-coated, stainless-steel wire electrodes was inserted into superficial dorsal neck muscles. Lead wires from the various recording sites were tunnelled beneath the skin to the back of the rat's head. Their ends were soldered to separate pins of a multi-pin sub-miniature socket. It was firmly fixed to the skull with dental acrylic cement. All incisions were brought together with 3/0 silk sutures after liberally dusting exposed tissue with Neomycin powder.

After full recovery from anaesthesia, a mating plug was inserted into the socket on the rat's skull. By means of a connecting cable, electrophysiological signals were fed to amplifying, filtering, signal-processing and pen-recording equipment. The amplifying and filtering modules used were Neurolog NL 103, 105 and 125. The settings for the filters were the same for all muscles tested - low-frequency 5 kHz, high-frequency 50 kHz with a 50 Hz notch filter incorporated in the circuit. The resulting e.m.g. signals were integrated using Grass 7P3 (RC) integrators with the time constant set at 20 ms. The e.m.g.s in their integrated form were displayed on separate channels of a Grass 7D polygraph. The integrators for the different muscles had the same frequency-filtering settings. A constant level of signal attenuation was maintained for each muscle for the duration of each experiment. The rat was placed in a 13 l Perspex box which was placed in a temperature-controlled experimental chamber. The Perspex box could be perfused with ambient air or selected gas mixtures during daytime recording sessions, and was large enough to allow the rat complete freedom of movement.

In the more detailed study of integrated e.m.g. activity recorded from thoracic cage muscles on the animal's right side, the external and internal interosseous muscles of the 2nd, 5th, 8th and 10th interspaces were implanted together with the parasternal muscles of the 2nd and 5th interspaces and the levator costae muscles of the 8th and 10th interspaces. Because of the marked variation in the size of the peak, integrated e.m.g. activity recorded from one non-r.e.m. sleep epoch to another in a given rat and from rat to rat, the 25th, 50th (median) and 75th percentiles were calculated rather than means and standard deviations. A minimum of eight measurements of peak, integrated e.m.g. activity was made while rats assumed each of three postures during non-r.e.m. sleep: curled to the right, curled to the left and facing directly forward, i.e. sphinx position, and as they breathed air, air enriched in CO₂ and air deficient in O₂. In the case of scalenus medius, the above treatment conditions were adopted but measurements were made while the rats assumed the well-curled-up posture (A), a less-curled-up posture (B), either to the left or to the right, and the open, extended posture, or sphinx position (C). Recordings were made from at least three rats when compiling data for the muscles of each intercostal interspace and the scalenus medius muscles. The percentiles were calculated for each rat separately, in each treatment condition. The median value from the readings on the three rats in each condition was computed and the resultant set of percentiles is presented in Figs. 1-3.

RESULTS

Initially all intrinsic and selected extrinsic muscles of the thoracic cage were surveyed to characterize their respiratory activity during sleep and wakefulness.

During non-r.e.m. sleep, those muscles attached to cephalic ribs, i.e. scalenus medius, the parasternals and the external and internal interosseus intercostal muscles of the 2nd and 3rd interspaces, always exhibited inspiratory activity. Expiratory activity was commonly encountered in both the external and internal intercostal muscles of the mid-thoracic region. In caudal interspaces, interosseous intercostal

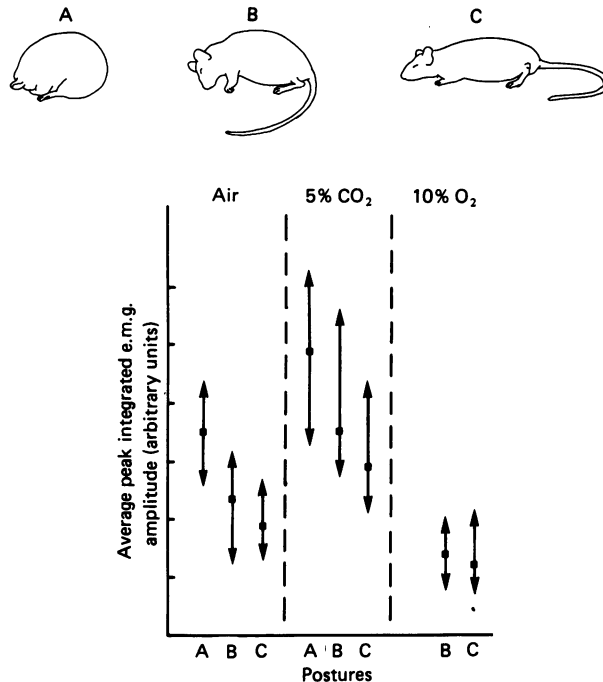


Fig 1. Median peak amplitude (50th percentile, filled squares) of the integrated e.m.g. of the right scalenus medius muscle (ordinate), during non-r.e.m. sleep, as a function of body postures as depicted at the top of the Figure (A, B and C) and the breathing of air, 5% CO₂ in air and 10% O₂ in N₂. Tip of upper arrow, 75th percentile; tip of lower arrow, 25th percentile.

and the levator costae muscles showed expiratory activity only occasionally. In general, expiratory activity was most likely to be present in the external intercostal muscles. Such activity was manifest during waking and extended, for a variable period, into non-r.e.m. sleep. A transition from expiratory to inspiratory activity could occur in non-r.e.m. sleep but if not, it always occurred at the onset of r.e.m. sleep regardless of the ribcage muscle under study.

Scalenus medius

This muscle exhibited inspiratory activity during non-r.e.m. sleep which was maximal in the well-curled-up posture, A, and less in more open and extended

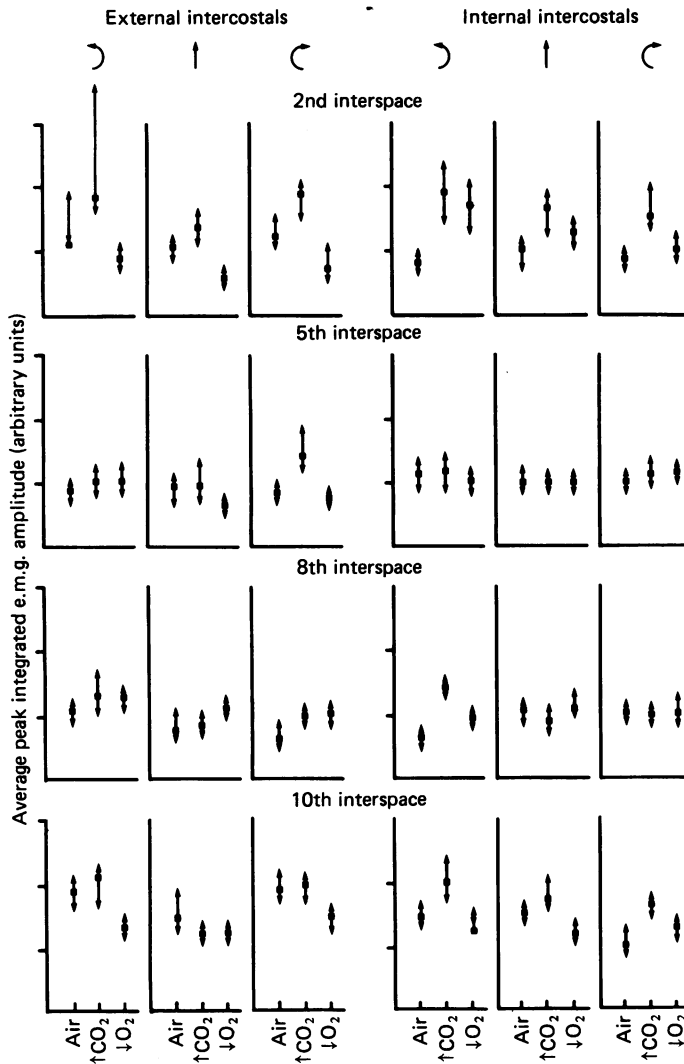


Fig. 2. Median peak amplitude (50th percentile) of the integrated e.m.g. (ordinate) of the external and internal intercostal muscles of the 2nd, 5th, 8th and 10th interspaces, on the right side, as a function of posture (curled-up to the left, sphinx position and curled-up to the right, as indicated at top of Figure) and the gas mixture breathed (air, 5% CO₂ in air and 10% O₂ in N₂, as indicated at bottom of Figure). All readings taken during non-r.e.m. sleep. See Fig. 1 for other details.

postures, B and C, respectively (Fig. 1). An underlying tonic activity was observed on some occasions, although it could not be related to any one posture or group of postures, i.e. lying on one side or the other. Compared with breathing air, the breathing of CO₂ resulted in increased inspiratory activity in scalenus medius for each of the main postures (Fig. 1). During hypoxic breathing, rats did not assume the A posture, and the magnitude of the muscle's output was decreased in both postures B and C when compared with breathing air.

External and internal (interosseous) intercostal muscles

Both the external and internal intercostal muscles exhibited chiefly *inspiratory* activity during non-r.e.m. sleep independent of the gas mixture breathed and the interspace from which recordings were made. In the 2nd interspace and during the breathing of CO₂, both muscle groups showed an increase in inspiratory activity, when compared with air-breathing conditions (Fig. 2). This activity was greater when

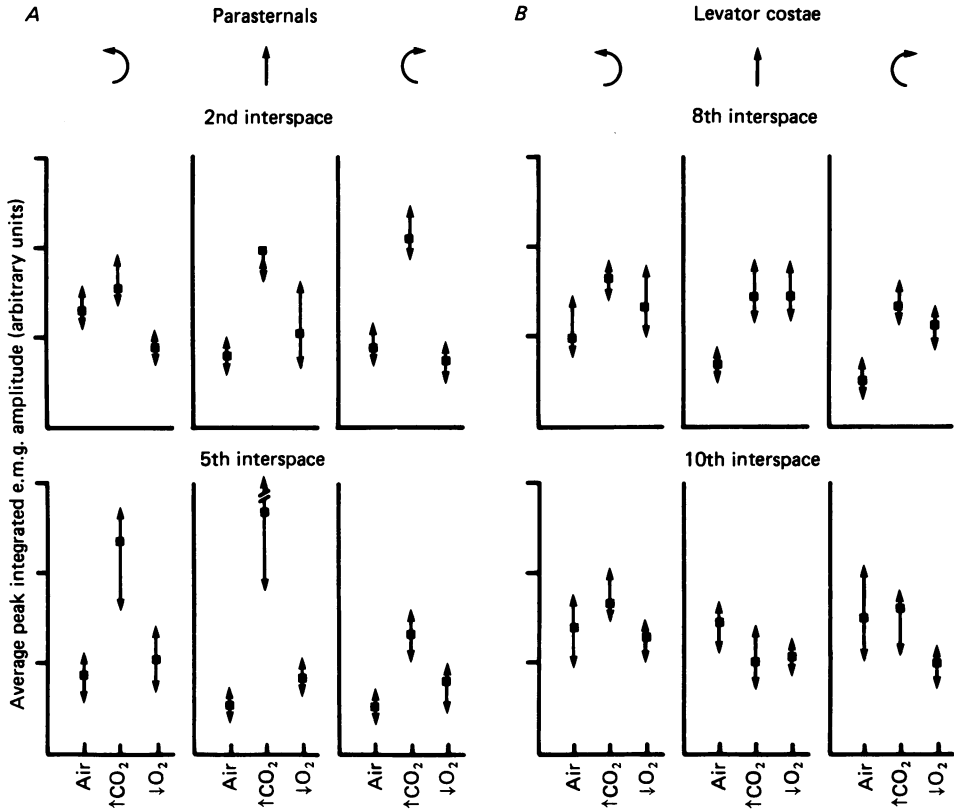


Fig. 3. Median peak amplitude (50th percentile) of the integrated e.m.g. of the parasternal muscles of the 2nd and 5th interspace (A) and of the levator costae of the 8th and 10th interspaces (B) as a function of posture (indicated at top of Figure) and gas mixture breathed (indicated at bottom of Figure). Electrodes inserted into muscles on the right side and measurements taken during non-r.e.m. sleep. See Fig. 2 for other details.

the rat was in the curled-up posture than in the sphinx position. In this space hypoxic breathing decreased the respiratory activity of the external intercostal but tended to enhance the activity of the internal intercostal muscle. In the 5th and 8th interspaces neither posture nor the gas mixture breathed altered the degree of muscle activity; there were occasional exceptions, e.g. external intercostal of the 5th interspace increased its respiratory activity when rats were curled-up to the right and breathing CO₂ (Fig. 2). In the 10th interspace the external intercostal was more active when the animal was curled-up and the internal intercostal was augmented by CO₂.

Parasternal muscles

In the 2nd and 5th interspaces these muscles manifested activity during non-r.e.m. sleep which was always inspiratory. CO₂ breathing increased this activity when compared with air-breathing conditions (Fig. 3A). Hypoxic breathing either depressed, augmented slightly or had no effect on respiratory activity. Posture did not affect the parasternal muscles in the 2nd and 5th interspaces.

Levator costae muscles

In the 8th and 10th interspaces this muscle commonly showed inspiratory activity during non-r.e.m. sleep. During both CO₂ and hypoxic breathing, respiratory activity in the 8th interspace increased when compared with air-breathing conditions (Fig. 3B). In the 10th interspace, there were no consistent effects on respiratory activity regardless of the gas mixture inspired. In both the 8th and 10th interspaces posture was not a factor in determining the degree of muscle electrical activity.

Variability of respiratory activity among thoracic cage muscles

The scalenus medius and parasternal muscles consistently exhibited activity in phase with the diaphragm during non-r.e.m. sleep. No exceptions were observed.

On the other hand, interosseous intercostal muscles, whether external or internal, as well as the levator costae muscles, showed marked variability in the same and different animals and as a function of the gas mixture breathed. The exception occurred in the internal and external intercostal muscles of the first three spaces where these muscles were always inspiratory. Fig. 4A-C illustrates recordings taken from the levator costae in the 9th and 10th interspaces in the same animal: both muscles showed expiratory activity during quiet wakefulness while breathing air (Fig. 4A) and in non-r.e.m. sleep breathing CO₂ (Fig. 4B). Fig. 4C shows that in the same animal these muscles can be inspiratory in non-r.e.m. sleep. Fig. 5 shows expiratory activity in the external intercostal muscles of the 8th and 9th interspaces during non-r.e.m. sleep.

The tonic component can be present or absent in any interspace as illustrated in Figs. 5-7. In Figs. 5 and 6 both the internal and external intercostal muscles of the 8th and 9th interspaces showed inspiratory activity superimposed on a degree of tonic activity during non-r.e.m. sleep. However, in Fig. 7, a tonic component was not observed in the same muscles of the 10th interspace during non-r.e.m. sleep. The presence or absence of tonic activity was not related to posture.

R.e.m. sleep

If a thoracic cage muscle exhibited tonic as well as respiratory phasic activity during non-r.e.m. sleep, the tonic activity always disappeared in r.e.m. sleep (Figs. 5 and 6). Respiratory phasic activity either disappeared, became weaker or was unaffected (Figs. 5-7). In those instances in which expiratory activity was present in a given muscle during non-r.e.m. sleep this activity always changed to inspiratory at the onset of r.e.m. sleep (Fig. 5). Expiratory activity was never recorded in any intrinsic chest wall muscle during r.e.m. sleep.

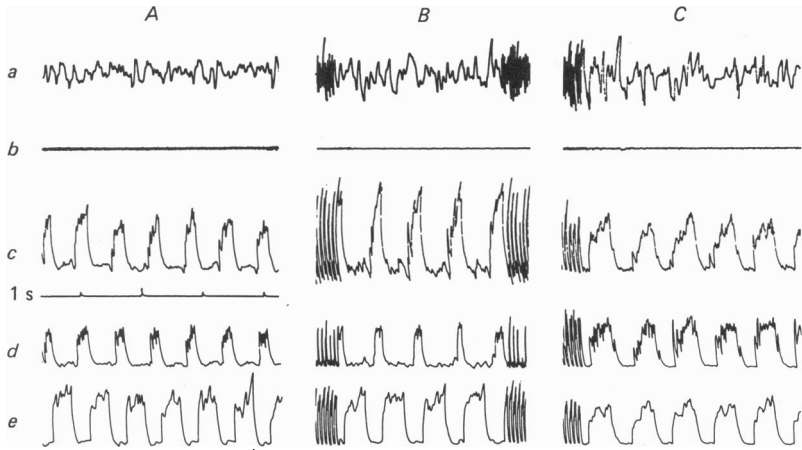


Fig. 4. Polygraphic recording from a single rat. *a*, electrocorticogram; *b*, dorsal neck e.m.g.; *c*, integrated e.m.g. of the levator costae of the 8th interspace; *d*, integrated e.m.g. of the levator costae of the 10th interspace; and *e*, integrated e.m.g. of the diaphragm during: *A*, wakefulness while breathing air; *B*, non-r.e.m. sleep while breathing 5% CO₂; and *C*, non-r.e.m. sleep while breathing air.

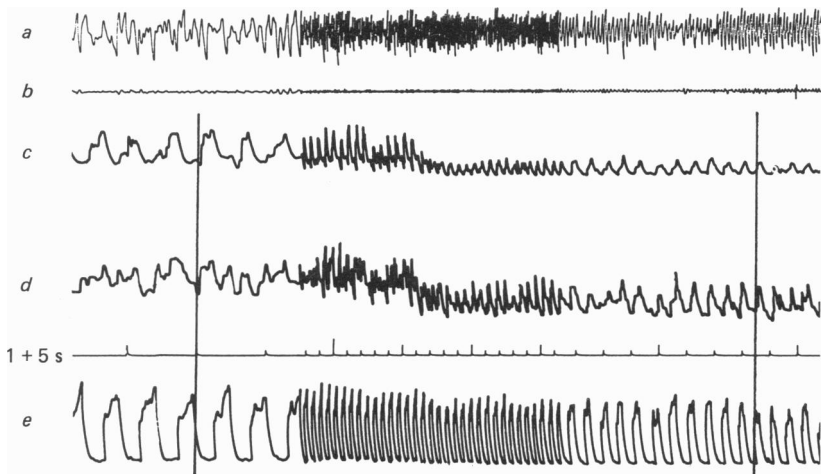


Fig. 5. Continuous polygraphic recording from a rat while breathing air in the transition from non-r.e.m. sleep (at left) into r.e.m. sleep (at right). *a*, electrocorticogram; *b*, dorsal neck e.m.g.; *c*, integrated e.m.g. of the external intercostal muscle of the 8th interspace; *d*, integrated e.m.g. of the external intercostal muscle of the 9th interspace; and *e*, integrated e.m.g. of the diaphragm. Vertical bar at left, onset of expiration; vertical bar at right, onset of inspiration.

DISCUSSION

Up to about two decades ago most investigators assumed that on the basis of the opposing orientation of their muscle fibres, the external intercostal muscles raise the ribcage, an inspiratory action, and the internal intercostal muscles depress it, an expiratory action. A considerable body of evidence seemed to support this hypothesis, i.e. Hamberger's theory (see Campbell, 1958, for review). Bronk & Ferguson (1935)

were the first to show that in the decerebrate cat the nerve supply to both the external and internal intercostal muscles can occasionally show activity coincident with inspiration. Subsequently, Boyd (1967, 1969) showed that the unanaesthetized rabbit exhibits either inspiratory or expiratory activity in *both* external and internal intercostal muscles depending, in part, on the site of e.m.g. recording electrodes. Le

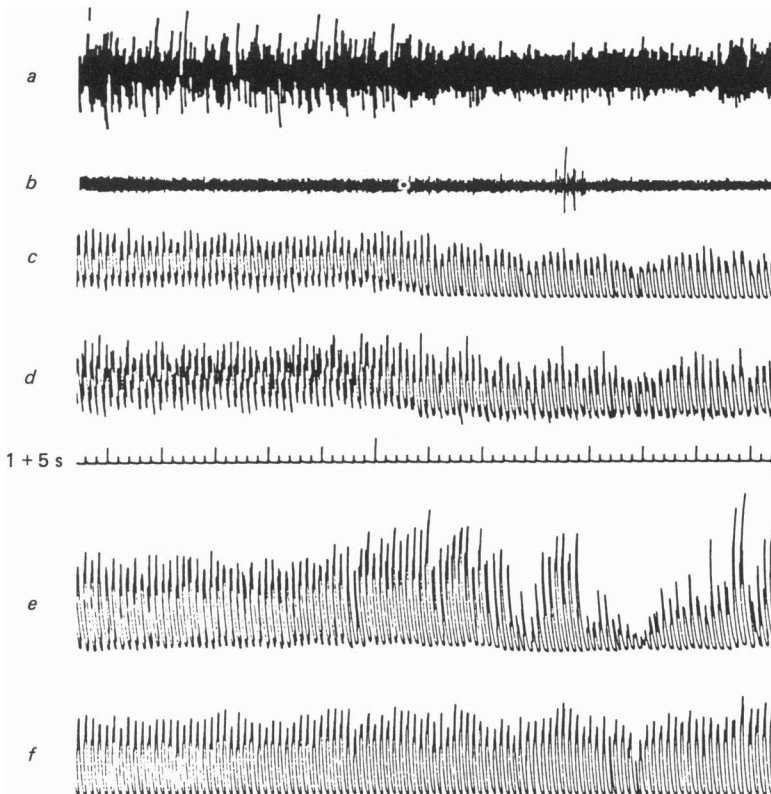


Fig. 6. Continuous polygraphic tracings from a rat breathing air in the transition from non-r.e.m. sleep (at left) into r.e.m. sleep (at right). *a*, electrocorticogram; *b*, dorsal neck electromyogram; *c*, integrated electromyogram of the internal intercostal muscle of the 8th interspace; *d*, integrated electromyogram of the external intercostal muscle of the 8th interspace; *e*, integrated electromyogram of the levator costae of the 8th interspace; and *f*, integrated electromyogram of the diaphragm. 1 + 5 s, 1 and 5 s time markers.

Bars & Duron (1984) have recently confirmed his findings in the cat: external and internal intercostal muscles act synergistically in the cephalic and caudal regions of the thoracic cage and antagonistically in the middle portion. It remained for De Troyer *et al.* (1985) to demonstrate in the dog that in spite of the different orientation of external and internal intercostal muscle fibres, their action on the ribs results in a net elevation at the functional residual capacity (F.R.C.).

Our study in the rat confirms and extends the above summary of findings in other species. It adds further support to the idea that Hamberger's theory is untenable (De Troyer *et al.* 1985; Saumarez, 1986). In addition, we have shown that the variability in respiratory response characteristics depends on the particular ribcage muscle under

study, the animal's state of consciousness, its posture and the gas mixture it breathes. Therefore, it is difficult to categorize the respiratory function of individual thoracic cage muscles. Nevertheless, this study shows that cephalic ribcage muscles (scalenus medius, parasternals and interosseous intercostal muscles) always exhibit inspiratory activity. On the other hand, those muscles of the mid-thoracic region, and less so those of the caudal region, may be inspiratory or expiratory. Whereas gas mixture and posture affect the degree of cephalic muscle respiratory activity, their effect on the intercostal and levator costae muscles in the caudal region is weak or absent. If an

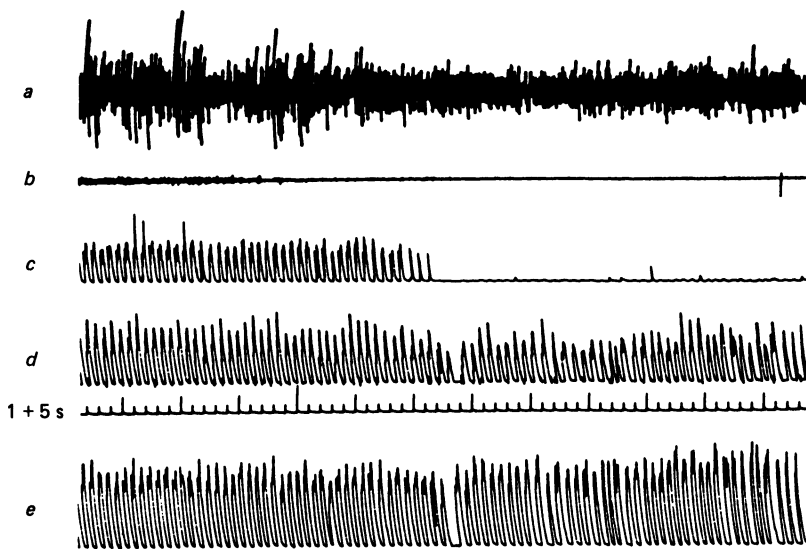


Fig. 7. Continuous polygraphic tracing from a rat breathing air in the transition from non-r.e.m. sleep (at left) into r.e.m. sleep (at right). *a*, electrocorticogram; *b*, dorsal neck e.m.g.; *c*, integrated e.m.g. of the external intercostal muscle of the 10th interspace; *d*, integrated e.m.g. of the internal intercostal muscle of the 10th interspace; and *e*, integrated e.m.g. of the diaphragm.

intercostal muscle manifests an expiratory pattern of activity during non-r.e.m. sleep, such activity either disappears or changes to the inspiratory phase at onset of r.e.m. sleep. Also, any tonic activity which is present during non-r.e.m. sleep disappears at the onset of r.e.m. sleep. Thus, ribcage muscles become less labile during r.e.m. sleep.

De Troyer *et al.* (1985) have shown that at the F.R.C., i.e. apnoea brought about by mechanical hyperventilation in the anaesthetized dog, activation of either the external or internal intercostal muscles results in a cephalad displacement of the ribs. When the F.R.C. is increased by increasing lung volume, stimulation of the external and internal intercostal muscles results in a depression of the ribcage. As tonic activity in intercostal muscles is unrelated to sleeping postures in the rat its presence must be explained. As mentioned above, De Troyer *et al.* (1985) have shown that when intercostal muscles are made to contract, they elevate or depress the ribcage depending on lung volume. Therefore, we postulate that tonic intercostal muscle activity has a role in determining the F.R.C. and thus whether the middle and lower

interosseous intercostal muscles are inspiratory or expiratory. The evidence to support this proposition is as follows. (a) Expiratory activity in both external and internal intercostal muscles in middle and lower interspaces occurs only during quiet wakefulness and non-r.e.m. sleep when lung volumes are more likely to be high. In r.e.m. sleep, however, when tonic activity is absent and intercostal muscles are exclusively inspiratory, the lung volume is undoubtedly minimal. (b) The breathing of gas mixtures enriched in CO₂ or deficient in O₂ has a minimal effect on tonic intercostal muscle activity during non-r.e.m. sleep. (c) External and internal interosseous intercostal muscles in upper interspaces are exclusively inspiratory, regardless of the states of consciousness. The latter muscles, which have a minimal influence in setting the F.R.C., have the major role of elevating the ribcage in conjunction with that of scalenus medius and sternohyoid.

Goldman *et al.* (1985) in awake man and Dick *et al.* (1984) in the sleeping cat have demonstrated that posture affects the degree of respiratory activity in middle and lower thoracic intercostal muscles. We are unable to confirm their findings in the sleeping rat free to adopt different postures. However, there is a clear-cut influence of posture on the respiratory activity of scalenus medius and to some extent in the parasternal and interosseous intercostal muscles of upper thoracic interspaces (Figs. 1 and 2). It may well be that the difference in findings is explained by the use of different species.

The assertion is often made that muscles attached to ribs decrease both their tonic activity and their respiratory-related activity during r.e.m. sleep (Parmeggiani & Sabattini, 1972; Tusiewicz *et al.* 1977). Although we can confirm that tonic activity disappears when the rat enters r.e.m. sleep (Figs. 5 and 6), this is not always the case for respiratory-related phasic activity of these muscles. However, if an intercostal muscle in the rat exhibits *expiratory* activity during non-r.e.m. sleep, it always disappears and may even be replaced by inspiratory activity in r.e.m. sleep (Fig. 5). On the other hand, when inspiratory activity is present during non-r.e.m. sleep, that activity can continue largely unchanged, e.g. levator costae, 10th interspace (Fig. 7), decrease (Fig. 6, levator costae, 8th interspace) or totally disappear (Fig. 7, external intercostal, 10th interspace). Because frequency and tidal volume are highly variable during r.e.m. sleep in the rat, no generalizations can be made as to whether or not a ribcage muscle loses its respiratory action during r.e.m. sleep. Duron & Marlot (1980) have also shown that the triangularis sterni muscle of the cat sustains its expiratory activity during r.e.m. sleep. The fact that some thoracic cage muscles lose their inspiratory activity during r.e.m. sleep, while others do not, supports the idea that these muscles behave in a non-uniform and unpredictable manner during this phase of sleep. This is consistent with recent studies of upper-airway muscles of the rat: where the genioglossus and sternothyroid muscles lose their inspiratory activity at entry into r.e.m. sleep (Megirian *et al.* 1985), the sternohyoid and inferior pharyngeal constrictor muscles do not (Sherrey *et al.* 1986). Because many more respiratory muscles have been studied in great detail in the rat during sleep than in any other species, there is a need to extend studies of respiratory muscles to other mammals to learn whether they use different strategies during both non-r.e.m. and r.e.m. sleep to achieve optimum gas exchange.

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