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HUMAN DIAPHRAGMATIC ENDURANCE DURING DIFFERENT MAXIMAL RESPIRATORY EFFORTS

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SUMMARY

1. This study assessed human diaphragmatic endurance under two conditions: during maximal inspiratory efforts (with minimal elevation of abdominal pressure) and during maximal expulsive efforts (with minimal elevation of pleural pressure). Performance was compared with that of the flexors of the elbow.

2. In series of eighteen sustained maximal efforts begun near functional residual capacity the decline in trans-diaphragmatic pressure was significantly greater during the expulsive than the inspiratory efforts ($P < 0.01$). Diaphragmatic endurance was greater than that of the flexors of the elbow.

3. Electromyograms recorded during maximal and submaximal expulsive contractions indicated that the relatively rapid decline in abdominal pressure during the series of expulsive contractions reflected fatigue of the diaphragm rather than the abdominal muscles. Supramaximal phrenic nerve stimulation was used to check that complete activation of the phrenic motoneurone pool could be achieved during series of maximal expulsive efforts.

4. It is concluded that the reduced endurance capacity of the diaphragm during expulsive efforts did not reflect peripheral failure of the abdominal muscles or an inability to activate the diaphragm fully during those maximal efforts.

5. The deterioration in diaphragmatic performance when abdominal pressure is elevated may be due to an impairment of muscle perfusion.

INTRODUCTION

There is controversy about the relative endurance of human inspiratory and limb muscles. Roussos & Macklem (1977) found that during resistive loading subjects were able to maintain about 40% of their maximal trans-diaphragmatic pressure. Maximal elevation of this pressure requires simultaneous generation of a positive intra-abdominal pressure (by co-contraction of the diaphragm and abdominal muscles) and a negative pleural pressure (by recruitment of inspiratory intercostal and accessory muscles). Bellemare & Grassino (1982) used a similar technique to document the performance of the diaphragm. Both groups concluded that diaphragmatic performance is the same as that of a limb muscle during phasic work.

The possibility that fatigue of abdominal muscles may have contributed to the decline in trans-diaphragmatic pressure was not considered.

By contrast, studies of isolated muscles suggest that the diaphragm has endurance properties which exceed those of a limb muscle of mixed fibre type (e.g. Lee, Guenther & Meleney, 1916; Faulkner, Maxwell, Ruff & White, 1979; Gandevia, McKenzie & Neering, 1983; Pagala, Namba & Grob, 1984). In addition, data from other studies are consistent with the view that human inspiratory muscles are relatively resistant to fatigue. During sustained isocapnic hyperpnoea (Freedman, 1966; Tenney & Reese, 1968; Leith & Bradley, 1976) and inspiratory loading (Roussos, Fixley, Gross & Macklem, 1979; Nickerson & Keens, 1982) subjects can maintain indefinitely 55–70% of their maximal inspiratory performance. This value exceeds the endurance of limb muscles performing phasic work (Monod & Scherrer, 1965). In a direct comparison of the performance of respiratory and limb muscles using maximal isometric contractions, Gandevia *et al.* (1983) found that the inspiratory muscles had a greater capacity for endurance than the muscles acting at the elbow joint. This could not be explained by rotation of activity between synergistic inspiratory muscles or failure to activate the phrenic motoneurone pool fully (Gandevia & McKenzie, 1985; see also Bellemare & Bigland-Ritchie, 1984; Gandevia & Rothwell, 1987). In the tasks which revealed enhanced endurance of the inspiratory muscles large negative pleural pressures are generated with minimal elevation of abdominal pressure.

To explain the discrepancy between the assessment of inspiratory muscle endurance during a manoeuvre which elevates abdominal pressure (Roussos & Macklem, 1977; Bellemare & Grassino, 1982) and one which does not (e.g. Gandevia *el al.* 1983) we postulated that endurance of the diaphragm may be impaired during manoeuvres which elevate abdominal pressure. Therefore, endurance has been measured during series of maximal Mueller manoeuvres ('pure' inspiratory efforts with minimal elevation of abdominal pressure), and maximal expulsive efforts (performed with minimal elevation of intrathoracic pressure). In both manoeuvres the phrenic motoneurone pool can be activated maximally (Gandevia & McKenzie, 1985). The performance of a control limb muscle group was also studied. A preliminary account of some of this work has been published (McKenzie & Gandevia, 1985*b*).

METHODS

The experiments were designed to measure endurance of the diaphragm during two different types of voluntary contraction: pure inspiratory manoeuvres and expulsive manoeuvres. We did not use the combined expulsive–Mueller manoeuvre because there is commonly variable activation of muscle groups on both sides of the diaphragm (Gibson, Clark & Pride, 1981; De Troyer & Estenne, 1981). In the same subjects, performance of the diaphragm was compared with that of the flexors of the elbow. Additional studies were performed (i) to assess the extent of voluntary activation of the relevant motoneurone pools during the respective manoeuvres, and (ii) to determine whether geometric factors might account for observed differences in trans-diaphragmatic pressure.

Subjects

Twenty experiments were performed on ten healthy male subjects ranging in age from 19 to 34 years. They included eight volunteers who were not familiar with respiratory investigations or the purpose of the study. Six subjects participated in the major study which involved endurance tests of the diaphragm and flexors of the elbow and in which each subject was studied on at least two occasions. Subjects gave informed consent and the study was approved by the appropriate institutional ethics committees.

Tests of the elbow flexors

Maximal voluntary contractions of the elbow flexors were performed with the subject seated and the dominant arm (fully supinated and the elbow flexed at 90 deg) fixed to an isometric myograph (see Gandevia *et al.* 1983). Torque was measured continuously and displayed to the subject. Prior to the endurance test three to five brief maximal efforts were performed until reproducible values ($\pm 5\%$) were obtained. After a rest of 15 min the subject performed the endurance test which consisted of eighteen maximal voluntary contractions sustained for 10 s and separated by rest intervals of 10 s (i.e. duty cycle 50%). Throughout each contraction subjects were loudly exhorted to maintain a maximal effort. Endurance was measured as the ratio of the peak (or average) force attained in the better of the last two contractions and the peak (or average) value in the better of the first two contractions. It was expressed as a percentage. Values for average force sustained throughout each contraction were obtained with a digital planimeter.

Diaphragmatic manoeuvres

Diaphragmatic endurance was assessed using inspiratory efforts (against a closed airway) and expulsive manoeuvres (performed with the glottis open). To control diaphragmatic length, antero-posterior diameters of the rib-cage and abdomen were monitored using pairs of linearized magnetometers at the height of the nipples and just above the umbilicus (Konno & Mead, 1967). Subjects viewed the diameters as an X–Y plot so that diaphragmatic contractions could be performed with a similar thoraco-abdominal configuration (Fig. 1). The position of the relaxation curve and the resting end-expiratory level were checked regularly without visual feed-back to the subject. To minimize changes in spinal attitude subjects wore a rigid spinal brace strapped to the shoulders and hips. A multi-lumen gastro-oesophageal catheter was used to record gastric pressure (P_{ab}) and mid-oesophageal pressures (P_{pl}) and, in some experiments, diaphragmatic EMG (McKenzie & Gandevia, 1985*a*; Gandevia & McKenzie, 1985).

Prior to the endurance tests subjects made inspiratory and expulsive efforts with visual feed-back of P_{ab} and P_{pl} and with the thoraco-abdominal configuration close to the relaxed end-expiratory level. During inspiratory efforts, against a closed airway, the subject developed a maximal reduction in P_{pl} while maintaining P_{ab} close to the resting level. To allow for changes in lung volume due to gas expansion, inspiratory efforts were commenced about 500 ml below functional residual capacity. This volume was based on a functional residual capacity of 3·5 l and maximal inspiratory pressure of 120 cmH$_2$O. Because maximal inspiratory efforts distort the shape of the rib-cage (e.g. Saunders, Kreitzer & Ingram, 1979) subjects kept the abdominal diameter close to the relaxed end-expiratory position. Expulsive efforts were commenced at the end-expiratory level and the subject kept the 'relaxed' rib-cage diameter at the relaxed end-expiratory position. To maintain glottic patency during maximal expulsive manoeuvres, subjects were initially instructed to pant, but most learnt to avoid glottic closure without air movement. Satisfactory training of subjects required 30–50 min, and was followed by a 20 min rest period.

The subject then performed an endurance test with series of maximal inspiratory or expulsive efforts following the same protocol described for the flexors of the elbow. After a further rest period of at least 30 min endurance was assessed using the other respiratory manoeuvre. The order of testing varied between subjects. Maximal voluntary pressures at the start of the second endurance test were similar to those obtained with the same manoeuvre prior to the first endurance test. For each contraction the peak and average pressures were measured.

Electrophysiological studies of diaphragmatic fatigue and activation

In one set of studies in four subjects electromyographic activity of the diaphragm and abdominal muscles was recorded during several prolonged (2–5 min) submaximal expulsive efforts at 20–40% of a maximal voluntary contraction. Contractions were performed as described above except that the subject was shown also a 'target' abdominal pressure on an oscilloscope. Subjects continued to breathe during contractions by panting until they could no longer maintain the target abdominal pressure. Surface recordings of abdominal muscle EMG were made with skin-mounted preamplifiers placed over the external oblique (anterior axillary line, midway between the costal margin and the iliac crest). The interelectrode distance was 15 mm. In some experiments EMG was recorded simultaneously from several sites over the abdominal wall, including over rectus abdominus. Rectified EMG (bandwidth 8–800 Hz) was monitored on an oscilloscope and an ink-jet recorder with a frequency response over 1000 Hz.

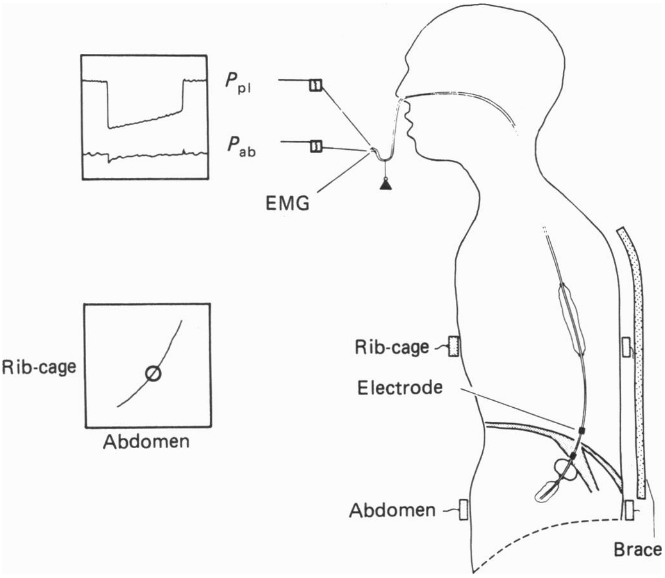

Fig. 1. Experimental set-up illustrating multi-lumen catheter stabilized by balloon at gastro-oesophageal junction and an external weight. Standard respiratory balloons recorded pleural (P_{pl}) and abdominal (P_{ab}) pressures. Electrodes attached to the catheter were used to record diaphragmatic EMG. Magnetometers measured antero-posterior diameters of rib-cage and abdomen. An orthopaedic spinal brace was used to limit changes in spinal attitude. Pleural and abdominal pressures, and rib-cage and abdominal diameters, were displayed to the subject on oscilloscope screens.

Because oesophageal recordings of diaphragmatic EMG are subject to systematic artifactual changes in amplitude with alterations in lung volume and thoraco-abdominal configuration (Gandevia & McKenzie, 1986), supramaximal stimuli were delivered to the phrenic nerve at 5 or 10 s intervals during control conditions and during the prolonged submaximal expulsive efforts. Changes in the area subtended by the negative and positive phases of maximal compound muscle action potentials (measured with a digital planimeter) were used to assess whether changes in the on-going rectified diaphragmatic EMG could be accounted for by changes in recording conditions. Rectified EMG was integrated for fixed periods (200–400 ms) which did not contain ECG artifact. The phrenic nerve was stimulated at the level of the cricoid cartilage with an adjustable probe electrode mounted on a firm neck brace. The electrode position was adjusted so that supramaximal stimuli (100–500 μs duration, up to 50 mA or 300 V) were delivered at 1·5–2 times the intensity required to produce a compound muscle action potential of maximal amplitude.

Finally, in two subjects the technique of twitch interpolation was used to check that the phrenic motoneurone pool could be maximally activated throughout the respiratory manoeuvres (e.g. Merton, 1954; Belanger & McComas, 1981; see also Bigland-Ritchie, 1981). Single supramaximal stimuli were delivered to the phrenic nerve as described above before, during and after the usual series of eighteen maximal expulsive efforts. The stimuli were given without warning during every second or third contraction. The peak and average pressures during these series of expulsive efforts were the same as those previously documented for these subjects and the relative decline over the series was comparable to that of the group. This technique has been previously used to document maximal voluntary activation of the diaphragm during maximal respiratory efforts (Bellemare & Bigland-Ritchie, 1984; Gandevia & McKenzie, 1985).

Statistics

Unless otherwise stated results are quoted as the mean ± one standard deviation. Differences between the relative endurance of the diaphragm during the two manoeuvres and between the diaphragm and the flexors of the elbow were tested by analysis of variance and covariance using the MANOVA program from SPSSx (Statistical Package for Social Sciences). Separate analyses were performed using the values for initial peak and average sustained force for the eighteen contractions. To control for the variation in strength between subjects, values were normalized relative to the largest of the first three contractions. The logarithm of the normalized value was used to satisfy the linear model of the statistical program.

RESULTS

Maximal strength

During maximal inspiratory efforts performed near functional residual capacity the pleural pressure ranged from -101 to -159 cmH_2O for the group of subjects (mean -119 cmH_2O). The change in gastric pressure during maximal expulsive efforts performed at functional residual capacity with the glottis open ranged from $+155$ to $+287$ cmH_2O (mean $+200$ cmH_2O). These values are within the normal ranges established in this laboratory (e.g. Gandevia *et al.* 1983; McKenzie & Gandevia, 1986) and by others (e.g. Agostoni & Rahn, 1960; Laporta & Grassino, 1985). Because the phrenic motoneurone pool can be maximally activated during both inspiratory and expulsive manoeuvres the difference in static trans-diaphragmatic pressure generated during the two manoeuvres cannot be explained by different degrees of neural activation of the diaphragm (Gandevia & McKenzie, 1985). Presumably, it is related to geometric factors including differences in diaphragmatic shape during the manoeuvres.

The specific geometric factors responsible for the difference in trans-diaphragmatic pressures during maximal inspiratory and expulsive efforts are not well understood and will not be considered in detail. However, measurements from antero-posterior and lateral radiographs were made during maximal inspiratory and expulsive efforts and these showed that the increase in cross-sectional area of the lower thorax during inspiratory compared with expulsive efforts could account for approximately half the difference in maximal pressure if the diaphragm behaved as a simple piston. In addition, there are also differences in the angle of insertion and in the length of the zone of apposition of the diaphragmatic muscle fibres during the two manoeuvres. The important point here is that the initial peak voluntary pressures during the two manoeuvres were generated by maximal activity of the diaphragm.

Maximal torque produced by the flexors of the elbow ranged from 68 to 81 N m (mean 74 N m). These values are also within the normal range established in this laboratory (e.g. Gandevia *et al.* 1983; Colebatch, Gandevia & Spira, 1986).

Endurance

The peak and profile of pressure produced during maximal *inspiratory* efforts (with no increase in P_{ab}) declined less over the series of contractions than during maximal *expulsive* efforts (with little change in P_{pl}). The relative decline over both series of diaphragmatic contractions was less than that during contractions of the elbow flexors (Figs 2 and 3).

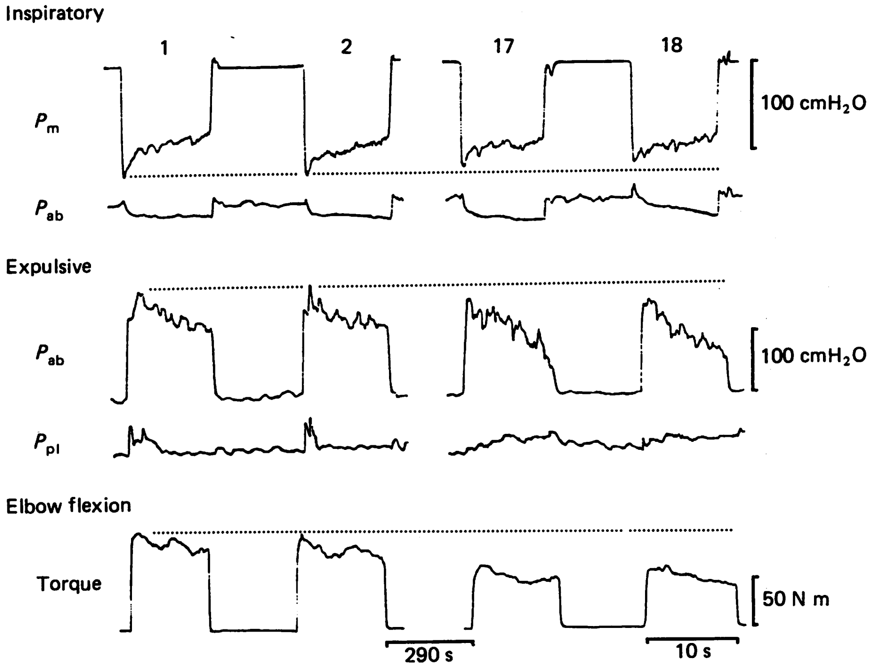

Fig. 2. Representative data obtained from one subject shows pressures during the first two and last two of a series of eighteen maximal static contractions (P_m: mouth pressure; P_{ab}: abdominal pressure; P_{pl}: pleural pressure). Inspiratory efforts: top traces; expulsive efforts: middle traces; torque developed by the flexors of the elbow during a similar series of contractions: bottom traces. The decline in force was greatest for elbow flexors and least for inspiratory efforts. For expulsive efforts the decline in force was intermediate between that of the other two manoeuvres.

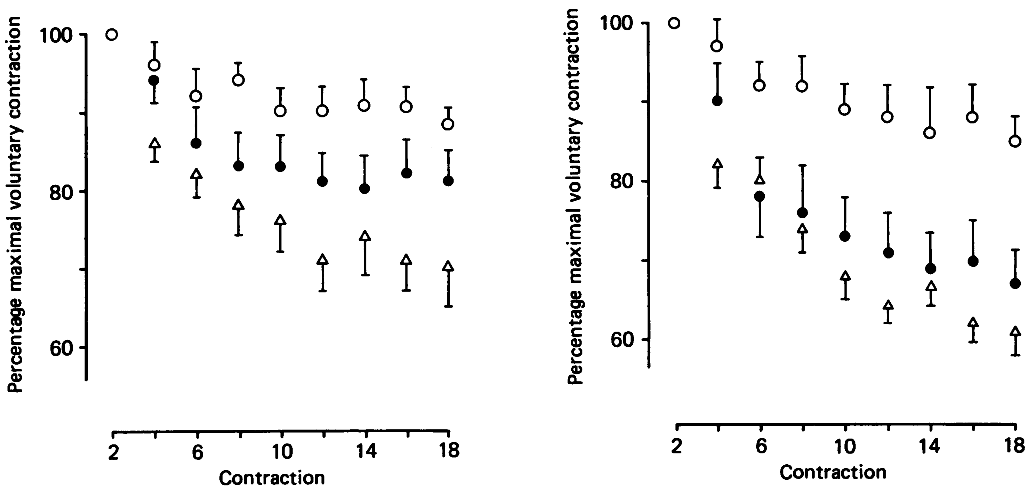

Fig. 3. Data from six subjects to show endurance during inspiratory efforts (○), expulsive efforts (●) and contractions of the elbow flexors (△). Each data point represents the peak force (left panel) or average force (right panel) during the better of each two consecutive contractions expressed as a percentage of that attained in the better of the first two (mean ± S.E.M.). The decline in force was greatest for elbow flexors and least for inspiratory efforts.

After eighteen contractions the average pressure (±S.D.) declined more during expulsive efforts (to 67±11·2% of its initial value) than during inspiratory efforts (85±7·9%, Fig. 3 at right). The relative decline in *peak* pressure showed the same trend but the difference was less: 81±8·9% for expulsive efforts and 88±6·1% for inspiratory efforts (Fig. 3 at left). This occurred in each subject. Statistical analyses (see Methods) revealed significant differences between the two diaphragmatic manoeuvres for measurements of both peak and average pressure over the eighteen contractions ($P < 0.001$). The decline in force (or pressure) was less during inspiratory efforts than during contractions of the elbow flexors (70±12·3% for peak flexor force and 61±6·7% for average force, Fig. 3). The decline in both peak and average force of the elbow flexors was greater than that for expulsive efforts but the difference was small ($P < 0.001$ for peak force, $P > 0.1$ for average force).

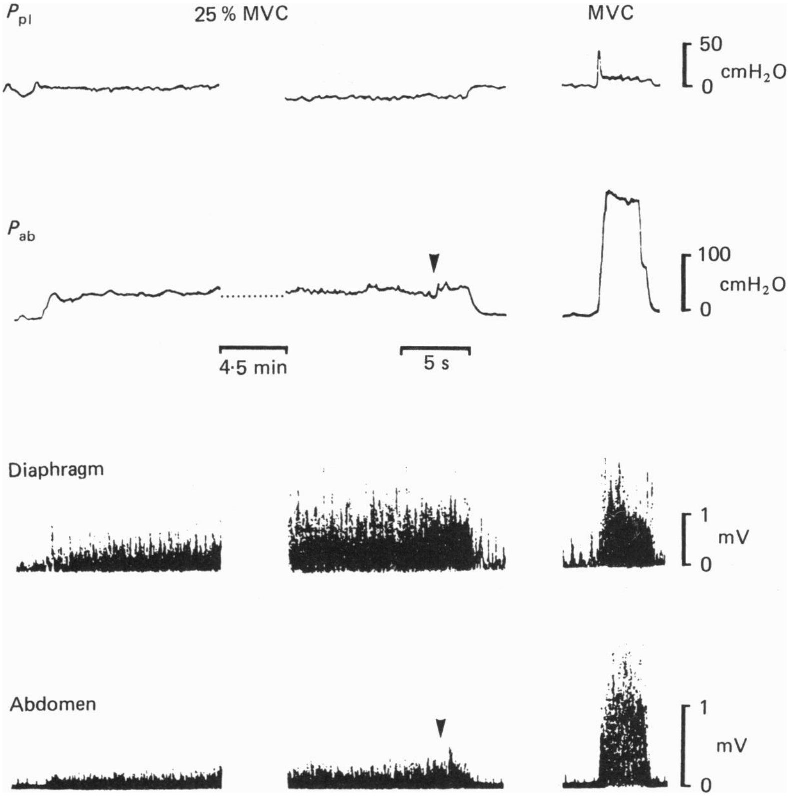

Fig. 4. Pleural pressure (P_{pl}), abdominal pressure (P_{ab}), rectified diaphragmatic EMG and abdominal muscle EMG at beginning (left traces) and end (middle traces) of a prolonged submaximal expulsive effort at 25% of a maximal voluntary contraction (25% MVC) and in an unfatigued maximal effort (MVC, right traces). Diaphragmatic EMG rose progressively to the maximal sustainable level while abdominal muscle EMG remained submaximal. At the arrow the subject was unable to maintain the 'target' pressure. The subsequent increase in pressure was accomplished by a burst of abdominal muscle EMG which resulted in displacement of the diaphragm.

Muscle fatigue and activation during expulsive manoeuvres

As the diaphragm and abdominal muscles act in series to elevate P_{ab} during expulsive efforts, a loss of force-generating capacity by either muscle might result in a decrease in pressure. To determine which of the muscles was likely to fatigue first under the present experimental conditions surface EMG of the diaphragm and abdominal muscles was recorded during series of maximal expulsive efforts and also during prolonged submaximal efforts.

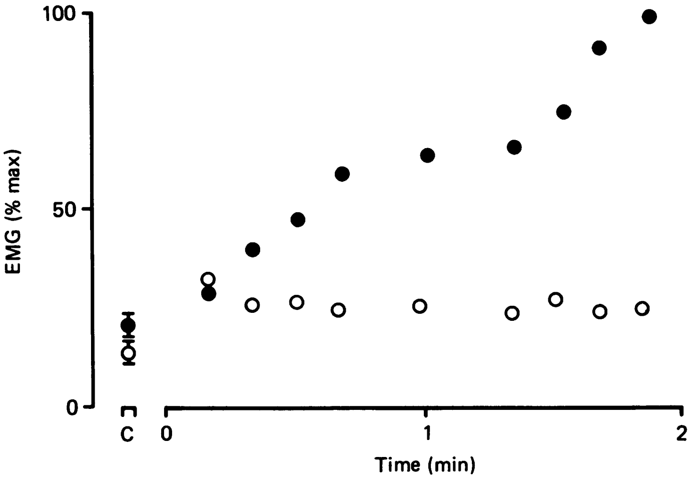

Fig. 5. Integrated diaphragmatic EMG (●, recorded with oesophageal electrodes) and abdominal muscle EMG (○) expressed as a percentage of the activity during a maximal expulsive effort performed with open glottis. Control values (C, ± S.D.) at left represent the peak activity during quiet breathing before and after the prolonged submaximal expulsive effort (30% maximal voluntary contraction). Supramaximal stimuli were delivered to one phrenic nerve at 10 s intervals. Values for diaphragmatic EMG were scaled according to the area of maximal compound muscle action potentials produced by phrenic nerve stimulation to allow correction for minor changes in recording conditions. The coefficient of variation for the amplitude and areas of these potentials was 15–20%. Two values are omitted because the diaphragmatic compound muscle action potential was contaminated by the ECG.

During series of maximal expulsive efforts in which substantial fatigue was documented, diaphragmatic EMG remained at, or near, maximal levels while abdominal muscle EMG usually changed in proportion to abdominal pressure. Thus it declined within each contraction as pressure declined after the initial peak and decreased as pressure declined during the series of contractions. Given the requirement to maintain a stable thoraco-abdominal configuration this decline in abdominal EMG is consistent with failure of the diaphragm to maintain its contractile force. Similar changes were observed for EMG recorded over external oblique and rectus abdominus.

During prolonged submaximal expulsive efforts (20–40% maximal voluntary contraction), abdominal EMG remained stable at levels of 20–30% of that during a maximal expulsive contraction with the glottis open. By contrast, diaphragmatic EMG rose progressively and at breaking point was close to that observed during a maximal expulsive effort (Fig. 4). This progressive increase in diaphragmatic activity was not due to a change in the relationship between the gastro-oesophageal recording electrodes and the diaphragmatic muscle fibres (Gandevia & McKenzie, 1986) because it remained after the rectified diaphragmatic EMG had been scaled according to the size of maximal compound muscle action potentials produced by

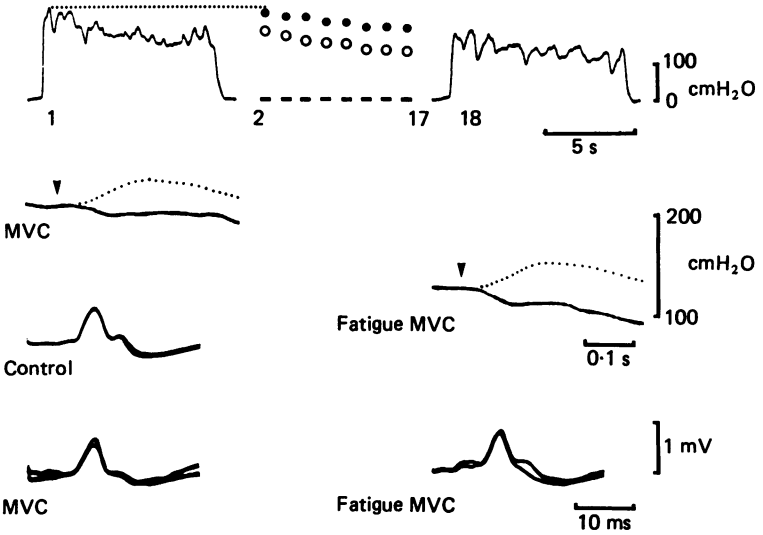

Fig. 6. Upper panels: recording of abdominal pressure (P_{ab}) for first and 18th expulsive effort during which supramaximal stimuli were delivered to the phrenic nerve (see text). Closed and open circles represent initial peak and average abdominal pressures for alternate intervening contractions. Dotted line indicates peak of first contraction. Middle panels: P_{ab} record at high gain shows no twitch response to stimulation (at arrow) during unfatigued maximal voluntary contraction (MVC, at left) and after substantial fatigue (Fatigue MVC, at right). Dotted lines represent control twitches at same gain. Calibration at right indicates absolute abdominal pressure for both traces. Lower panels: maximal compound muscle action potentials recorded before (Control) and during maximal voluntary contraction shown in middle panels. Each record shows two traces superimposed.

supramaximal stimulation of the phrenic nerve. For example, during a sustained expulsive effort (30% maximal voluntary contraction, Fig. 5) corrected diaphragmatic EMG rose approximately 10-fold to its maximal level. By contrast abdominal muscle EMG increased about 1·5-fold and remained at less than 20% of that recorded during maximal effort. The coefficient of variation for the area of maximal compound muscle action potentials recorded before, during and after the prolonged contraction was about 20%.

The ability to activate maximally the phrenic motoneurone pool during brief expulsive efforts (Gandevia & McKenzie, 1985) was confirmed in the present study. Furthermore, in two subjects whose performance in the endurance tests was similar to that of the group of subjects, electrophysiological evidence was obtained for maximal diaphragmatic activation at the start and end of a series of maximal expulsive contractions (Fig. 6). When supramaximal stimuli were delivered at random times during the series of contractions, superimposed trans-diaphragmatic 'twitches' were not observed when stimuli were delivered at the peak of an expulsive contraction. Twitches were observed when stimuli were delivered during one of the transient 'dips' in abdominal pressure but maximal activation was documented for 40% of the randomly interpolated stimuli. Complete activation of the phrenic motoneurone pool is not always achieved during inspiratory efforts when the diaphragm is fatigued (Gandevia & McKenzie, 1985) or during fatiguing expulsive contractions.

DISCUSSION

Development of a large intra-abdominal pressure was associated with decreased diaphragmatic endurance. This finding may resolve the disparity between previous findings of a resistance to fatigue during repeated maximal inspiratory efforts (Gandevia *et al.* 1983; McKenzie & Gandevia, 1986, 1987; confirmed here) and those of previous investigators who documented substantial diaphragmatic fatigue during resistive breathing using the combined expulsive–Mueller manoeuvre in which abdominal pressure rises (for example, Roussos & Macklem, 1977; Bellemare & Grassino, 1982). The present results suggest that diaphragmatic endurance depends on whether contraction of the diaphragm produces a negative intrathoracic pressure or a positive abdominal pressure.

Several aspects of diaphragmatic performance were considered to ensure that the manoeuvres used would provide a valid test of muscle endurance. First, manoeuvres were used in which co-operative subjects can maximally activate the relevant motoneurone pools (Gandevia & McKenzie, 1985). Secondly, during maximal diaphragmatic manoeuvres it is difficult to control the lengths at which the various synergistic muscles are contracting due to gas expansion and changes in thoraco-abdominal configuration. Thirdly, the contractile force of the human diaphragm can be measured only indirectly and, when large pressure changes are developed on both sides of the diaphragm, it is not possible to quantify the active component of the differential pressure (Gibson *et al.* 1981; De Troyer & Estenne, 1981). These potential difficulties are discussed below.

Recent studies have documented complete voluntary activation of the diaphragm during both maximal inspiratory and maximal expulsive efforts (Gandevia & McKenzie, 1985; see also Bellemare & Bigland-Ritchie, 1984). Complete activation during inspiratory and expulsive efforts can also be achieved in the presence of diaphragmatic fatigue (Gandevia & McKenzie, 1985; cf. Bellemare & Bigland-Ritchie, 1987). These findings alone suggest that the diaphragm is likely to be the limiting muscle during endurance tests involving the two manoeuvres. Because the extent of motor unit activation is maximal during the two diaphragmatic manoeuvres, contractile tension is presumably similar despite the greater maximal trans-diaphragmatic pressure generated in the expulsive compared with the inspiratory manoeuvre. Radiographic measurements in the present study suggest that simple geometric factors account for much of the difference in pressures generated by the two manoeuvres (also D. F. Rochester, unpublished observations).

During maximal respiratory manoeuvres it is difficult to control diaphragmatic length and to prevent passive transmission of pressure between the thorax and abdomen. These problems have been minimized for the endurance studies with the two diaphragmatic manoeuvres. Subjects maintained a minimal pressure change in one thoraco-abdominal compartment ('passive') while they developed a maximal pressure change in the other compartment ('active'). Trans-diaphragmatic pressure was then given by the pressure developed in the 'active' compartment. Distortion of the passive compartment was minimized. With lung volume and the antero-posterior dimension of the 'passive' compartment controlled, initial diaphragmatic length was probably maintained within a relatively small range during the different contractions. It is impossible to rule out some change in muscle length between and during the diaphragmatic manoeuvres studied here (Mead & Loring, 1982), but diaphragmatic endurance is not significantly affected when static inspiratory efforts are made at functional residual capacity plus half inspiratory capacity rather than at functional residual capacity (McKenzie & Gandevia, 1987).

Because a substantial decline in P_{ab} was observed during the series of maximal expulsive manoeuvres it was necessary to establish that this decline reflected predominantly diaphragmatic (rather than abdominal muscle) fatigue. Others have assumed, without any direct evidence, that a reduction in P_{ab} during a manoeuvre which involved the diaphragm was associated with diaphragmatic rather than abdominal muscle fatigue (e.g. Roussos & Macklem, 1977; Bellemare & Grassino, 1982). As P_{ab} declined during series of brief maximal expulsive manoeuvres, diaphragmatic EMG remained at maximal levels while activity of the abdominal muscles varied with fluctuations in abdominal pressure and remained submaximal. During prolonged submaximal expulsive efforts, abdominal muscle EMG increased relatively little while diaphragmatic EMG increased progressively and was close to its maximal level when the target pressure could not be maintained. This increase could not be explained by an artifactual change in recording conditions (e.g. closer apposition of the diaphragmatic muscle fibres to the oesophageal recording electrodes, Fig. 5). Thus during maximal expulsive efforts (with the glottis open) the abdominal muscles do not require the same degree of neural activation as the diaphragm. The reserve capacity to generate force presumably delays the onset of abdominal muscle fatigue during these manoeuvres.

One hypothesis to explain the finding that diaphragmatic endurance depends on whether the muscle develops a negative P_{pl} or a positive P_{ab} is that diaphragmatic perfusion is different under the two circumstances. For contractions above about 20% maximal voluntary contraction, intramuscular blood flow in limb muscles decreases progressively and probably ceases altogether above 70% maximal voluntary contraction (Humphreys & Lind, 1963). Force decline is greater during maximal voluntary contractions performed under ischaemic conditions (e.g. Merton, 1954). During maximal expulsive manoeuvres the thin sheet of diaphragmatic muscle is exposed to the large positive pressure developed in the abdominal compartment in addition to the raised intramuscular pressure due directly to active tension development. Abdominal pressure on average reaches +200 cmH$_2$O, in excess of the usual systolic pressure during maximal effort, so a reduction of diaphragmatic blood flow would be likely. By contrast, during inspiratory efforts the large negative intrathoracic pressure applied to the diaphragm may counteract the rise in intramuscular pressure and thus preserve blood flow especially on the thoracic surface of the diaphragm (see Kirkebø & Wisnes, 1982). Studies of diaphragmatic blood flow in anaesthetized dogs provide indirect support for this hypothesis (Buchler, Magder, Katsardis, Jammes & Roussos, 1985). The changes in human diaphragmatic endurance could not be explained by differences in systemic arterial pressure which was higher during maximal expulsive than inspiratory efforts (S. C. Gandevia & D. K. McKenzie, unpublished observations).

Diaphragmatic endurance during expulsive efforts approached that of the limb muscle studied despite the fact that the oxidative capacity and capillarity of the diaphragm is greater than that of most limb muscles in many mammalian species (Faulkner *et al.* 1979; Hoppeler, Mathieu, Krauer, Claasen, Armstrong & Weibel, 1981) and probably also in man (McKenzie, Gandevia & Shorey, 1983). The diaphragm also has a greater capacity to increase its blood flow than limb muscles (e.g. see Rochester & Bettini, 1976; Robertson, Foster & Johnson, 1977). These factors should endow the diaphragm with a high capacity for endurance. However, during maximal expulsive efforts the combination of the large positive abdominal pressure, the contractile tension and, perhaps, a reduction in cardiac output may result in a greater impairment of muscle function than that produced in a limb muscle during maximal static effort. Irrespective of the mechanisms involved, potential impairment of diaphragmatic performance during expulsive manoeuvres may explain why abdominal pressure is rarely elevated for prolonged periods during daily activities.

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