J. Physiol. (1955) 129, 12–26

AN ELECTROMYOGRAPHIC EXAMINATION OF THE ROLE OF THE INTERCOSTAL MUSCLES IN BREATHING IN MAN*

By E. J. M. CAMPBELL

From the Department of Physiology, Middlesex Hospital Medical School, W. 1

(*Received* 2 *November* 1954)

The intercostals are thin muscles, almost entirely covered by other muscles. There is no movement or action which is known to cause them to contract while the other muscles close to them are inactive. They are, therefore, difficult to examine electromyographically in the intact human subject because of the limitations of both surface and needle electrode techniques. This paper reports a series of experiments designed to overcome these difficulties and to establish the conditions under which intercostal activity occurs and its probable significance in respiration.

METHODS

Apparatus

Electromyograph. An Ediswan 4-channel electroencephalograph with inkwriters was used. The surface electrodes were shallow cups of silver coated with silver chloride. They were attached to the skin as described previously (Campbell & Green, 1953). The concentric needle electrodes were made from size 26 dental hypodermic needles and 42 s.w.g. copper wire, enamelled and single-silk covered. The wire was cemented into the needle with marco-resin S.B. 28 C. The shaft of the needle was earthed to the input of the electromyograph and the core was connected to one grid of the input, the other grid being earthed. The spirometer was a 6 l. water-filled Kendrick model, arranged to give a tracing on the electromyograph paper. When the recording paper was stationary the respiration trace was ahead of (to the left of) the electromyograph inkwriters by a distance which corresponds to 0·12 sec in the published records.

Apparatus for studying graded voluntary static inspiratory and expiratory pressures. The apparatus was essentially the same as that described previously (Campbell & Green, 1953). A differential manometer was connected to a side arm on the spirometer mouthpiece. The manometer could be set to any given pressure; the subject made an inspiratory (or expiratory) effort and balanced the manometer at the required pressure. The order of performance was randomized and the subject did not know what pressure he was exerting.

Observations were made under the following conditions: quiet breathing; progressively increasing pulmonary ventilation produced by rebreathing expired air from the spirometer; graded voluntary inspiratory and expiratory pressures; maximum voluntary inspiration and expiration. When the effects of increasing pulmonary ventilation due to asphyxia were examined the CO_2 absorber was removed from the spirometer circuit. Ventilation rates up to about 60 l./min due to

* Part of a thesis accepted for the Doctorate of Philosophy by the University of London.

CO_2 accumulation plus anoxia were produced in this way. Higher levels of ventilation were produced voluntarily. When the subjects were accustomed to the procedure they could produce a smooth progressive increase in ventilation (first involuntarily and then voluntarily) up to rates of over 100 l./min. The resistance of the apparatus was found to be without effect on the results even at high ventilation rates.

RESULTS

Examination of normal young male subjects with surface electrodes

Preliminary observations were made on two subjects from whom records were taken from the first eight intercostal spaces at many sites anteriorly and in the axilla. The findings were as follows:

(*a*) The records obtained from the second, third and fourth intercostal spaces resembled each other.

(*b*) The records obtained from the sixth, seventh and eighth intercostal spaces resembled each other.

(*c*) Activity was recorded from the first and fifth intercostal spaces during a large number of manoeuvres. Interpretation of the records was difficult because at both sites there are several muscles close to each other.

As a result of these findings three more subjects were studied from whom recordings were taken from the following sites: *The third intercostal space anteriorly.* A pair of electrodes 4·5 cm apart was placed with the medial electrode 3–6 cm from the midline. At this site the only muscles covering the intercostals are the pectoralis major and minor. *The sixth or seventh space antero-laterally.* A pair of electrodes 4·5 cm apart was placed straddling the anterior axillary line, the medial electrode being 12–13 cm from the midline and 6–7 cm obliquely up the intercostal space from the costal margin. At this site the only muscle covering the intercostals is the external oblique.

All the manoeuvres described in the section on methods were performed. A simultaneous recording from the external oblique muscle in the abdomen was also taken to enable the contribution of the external oblique to the electromyogram recorded over the intercostal space to be assessed.

The findings in the two preliminary subjects and the three subsequently examined will be described together.

The third intercostal space

The only significant respiratory activity recorded from this site was at the end of a deep inspiration (Fig. 1); it was associated with increased tautness of the axillary fold and therefore probably arose in the pectoralis major. During graded inspiratory and expiratory efforts and during increased pulmonary ventilation activity was only recorded at very high levels (Figs. 1 and 2).

The possible reasons for the failure to record significant respiratory activity in the upper intercostal spaces is discussed later.

The sixth and seventh spaces

Respiratory activity was much greater at these sites and the findings will be presented in more detail.

During quiet breathing and increased pulmonary ventilation (Fig. 1). Activity during inspiration was detected during quiet breathing in one subject, at ventilation rates of 24, 24·5 and 27 l./min in three. In the remaining subject no inspiratory activity was detected up to a ventilation rate of over 100 l./min.

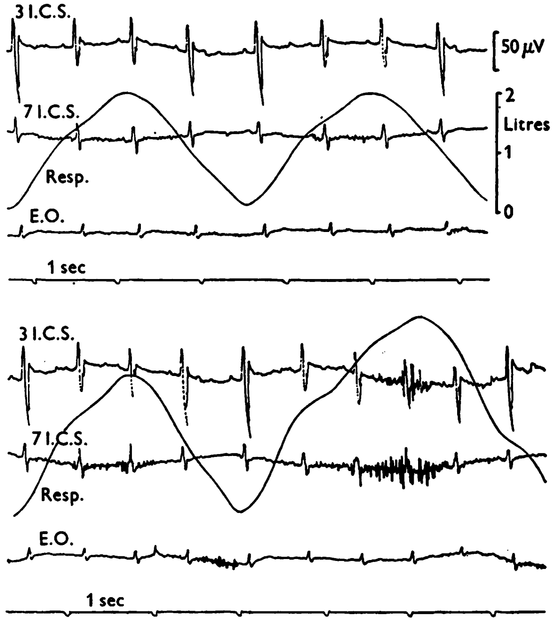

Fig. 1. The effects of increased pulmonary ventilation. Records taken with surface electrodes. Inspiration upwards. The subject rebreathed from a spirometer with no CO_2 absorber in the circuit. In the upper tracing the ventilation rate was 40 l./min and in the lower tracing 50–55 l./min. 3 I.C.S.—3rd intercostal space. Activity only present towards the end of the deep inspiration (tidal volume 3·25 l.) in the lower tracing. 7 I.C.S.—7th intercostal space. Definite inspiratory activity but no expiratory activity in both tracings. E.O.—external oblique (recorded from the abdominal wall). Definite expiratory activity but no inspiratory activity in both tracings.

No activity was detected over the external oblique in the abdominal wall during inspiration. Activity during expiration was not detected in quiet breathing. During increased pulmonary ventilation expiratory activity appeared in the intercostal record of the five subjects at the following ventilation rates: 92, 69, 80, 67 and 69 l./min. As expiratory activity always appeared in the external oblique at lower ventilation rates, the expiratory activity recorded over the intercostal spaces cannot be attributed to the intercostal muscles on this evidence.

During graded voluntary static inspiratory efforts (Fig. 2). Definite activity was recorded during efforts of -10 or -20 cm H_2O (that is during the maintenance of an intra-alveolar pressure 10 or 20 cm H_2O below atmospheric).

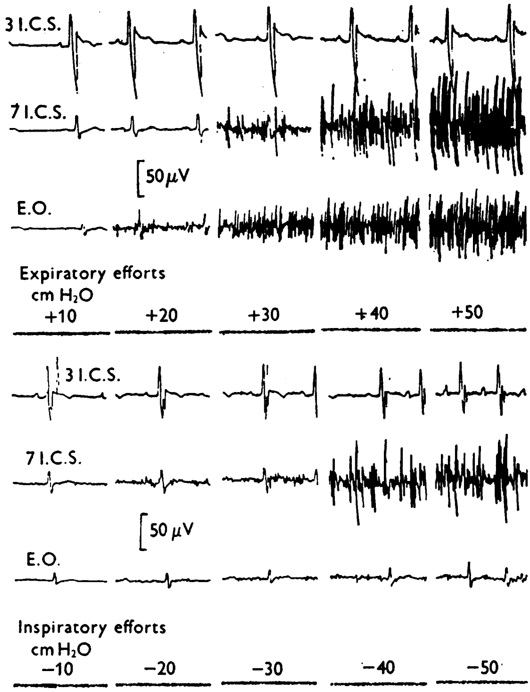

Fig. 2. Graded voluntary expiratory and inspiratory efforts. Records taken with surface electrodes. Each strip of tracing was taken while the subject was maintaining a constant intra-alveolar pressure. The pressures are related to atmospheric. 3 I.C.S.—3rd intercostal space. Slight activity at the higher pressures during both inspiratory and expiratory efforts. 7 I.C.S. —7th intercostal space. During expiratory efforts there was well-marked activity which was related in intensity to the magnitude of the pressure developed. The intensity of activity was not significantly greater than that recorded from the external oblique. During inspiratory efforts there was activity which was significantly greater than that recorded from the external oblique. E.O.—External oblique (recorded from the abdominal wall). During expiratory efforts there was marked activity related in intensity to the pressure. During inspiratory efforts there was slight activity, not related in intensity to pressure.

During greater efforts the electrical activity tended to be greater but its intensity was not as directly related to increasing effort as it was during expiratory efforts. The external oblique was usually inactive during this manoeuvre and never showed marked activity.

During graded voluntary static expiratory efforts. (Fig. 2). Activity was recorded which showed gradation in intensity directly related to the magnitude of the expiratory effort over a range from $+10$ to $+50$ cm H_2O. The activity was, however, never significantly greater than that recorded from the external oblique in the abdomen.

Further observations during quiet breathing

The observations reported above were made early in the study. It was decided to re-examine the lower intercostal spaces with surface electrodes employing minor refinements of electromyographic technique (increased amplification, decreased amplifier noise, increased recording paper speed, decreased interference from electrocardiogram) designed to give the best chance of detecting activity during quiet breathing. The sixth intercostal spaces of four young male subjects were examined. Rhythmic inspiratory activity was detected in all the subjects. The peak-to-peak amplitude of the potential recorded was 3–10μV.

Observations on women with radical mastectomies

As described above, no activity was recorded from the upper (second, third, fourth) intercostal spaces of young normal male subjects. Five women were, therefore, examined in whom either the whole of the pectoral muscles or all the muscle below the third rib had been removed. The intercostal spaces were easily palpable; only a few millimetres of skin and thin subcutaneous tissues separated the electrodes from the intercostal muscles.

In two of the subjects there was definite inspiratory activity in the upper intercostals during quiet breathing, and in two activity was possibly present during quiet breathing. In all of them inspiratory activity became definite when the pulmonary ventilation was only moderately increased (to about 15 l./min).

In none of them was there expiratory activity during quiet breathing. Expiratory activity did not appear during increased pulmonary ventilation until there was obvious distress. Two women achieved ventilation rates of over 50 l./min and 30 l./min respectively with no expiratory activity (Fig. 3).

In four of them expiratory efforts such as coughing or Valsalva's manoeuvre were associated with definite activity. (The findings in the fifth subject were doubtful.)

The patterns of activity in the upper and lower intercostal spaces were similar but the intensity of the recorded activity was greater in the lower spaces, the explanation may be that the muscles are thicker or the motor units are larger in the lower spaces. This evidence is further discussed later.

Observations on dyspnoeic patients

Four patients were studied who were dyspnoeic at rest and showed marked use of the accessory muscles of respiration. They were all very thin and their intercostal spaces were easily palpable. (The chest wall of one of them was subsequently found to be only 1 cm thick from skin to pleura in the second intercostal space.) Recordings were taken from both the upper (second, third, fourth) and lower (sixth, seventh, eighth) spaces in three of them.

They all showed inspiratory activity but no expiratory activity during quiet breathing. The intensity of the activity in the upper spaces was surprisingly small when compared with the palpable tautening in the intercostal space that occurred during inspiration. This tautening was therefore attributed mainly to the elevation of the first rib by the accessory muscles of inspiration.

It was not possible to obtain satisfactory records during the other respiratory manoeuvres.

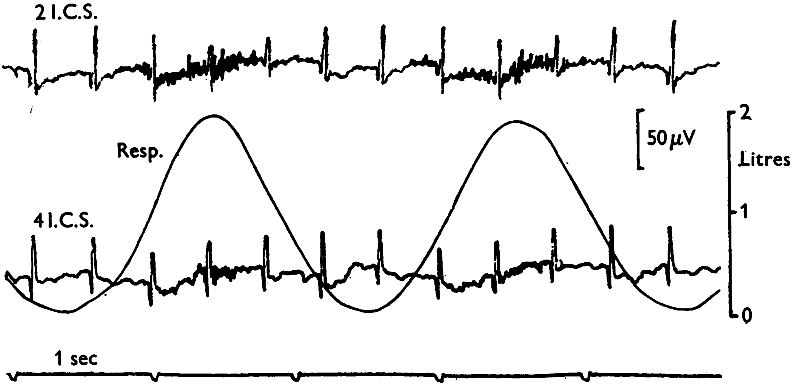

Fig. 3. Recordings from the intercostal spaces after radical mastectomy. Records taken with surface electrodes from the second and fourth intercostal spaces (I.C.S.) of a woman whose pectoral muscles had been removed 10 days previously. She rebreathed expired air from the spirometer. Inspiration is upwards. The ventilation rate was 53 l./min. There was definite inspiratory activity but no detectable expiratory activity.

The findings already described suggest that the failure to record intercostal activity from the upper intercostal spaces of young normal subjects with surface electrodes may be due to any or all of the following factors: the thickness of the overlying tissues; less activity in the intercostal muscles of the upper spaces; smaller motor units in the upper spaces.

Exploration with needle electrodes

The second and sixth intercostal spaces of one subject were explored with a concentric needle electrode. The skin and subcutaneous tissues were anaesthetized with 2 % lignocaine hydrochloride (B.P.). The needle was inserted until the resistance of the intercostal membrane was passed. Records were then taken with various minor adjustments of the position of the needle. Intercostal activity was most readily detected if the needle was first inserted until pleuritic pain was felt and then withdrawn slightly.

Findings in the second intercostal space. No definite inspiratory or expiratory activity was detected. It cannot be inferred that the intercostal muscles in this region are entirely inactive because it is difficult to be certain that the exploration was adequate. However, the relative ease with which intercostal activity was detected in the sixth space and the findings with surface electrodes make it probable that the intercostal muscles are less active in the upper than in the lower intercostal spaces of young male subjects.

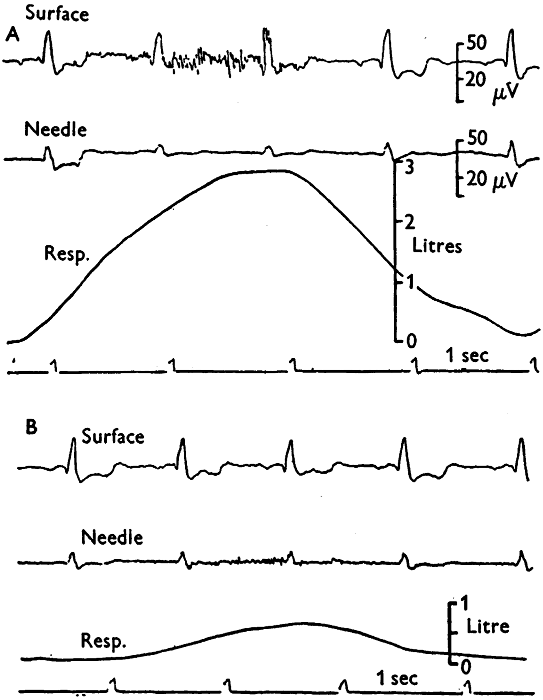

Fig. 4. Simultaneous recording with surface and needle electrodes. Localization of the needle electrode. Young male subject. A pair of surface electrodes was placed 4·5 cm apart in the sixth intercostal space; a concentric needle electrode was inserted midway between the surface electrodes. In both records the needle electrode was in the intercostal space deep to the external oblique. Between the upper and lower tracings the needle was inserted about 2 mm deeper into the space. The upper tracing showed intercostal activity in the surface record but not in the needle record during an inspiration of 3 l. The lower tracing showed activity in the needle record during an inspiration of 0·5 l. This activity was just detectable in the surface record.

Findings in the sixth intercostal space. Fig. 4 shows the influence of the position of the needle electrode. In A the needle electrode was deep to the intercostal membrane; no activity was detected during an inspiration of 3 l. although the surface record showed marked activity. Between A and B the needle was inserted 1–3 mm further into the intercostal space. B shows an inspiration of 0·5 l. with definite activity in the needle record which is barely discernible in the surface record. Fig. 4 thus demonstrates the small range of this type of needle electrode and the difficulty of localizing it in a thin muscle.

With the electrodes in this intercostal space the only muscles whose activity could be recorded are the intercostals and the external oblique. The latter can be excluded for the following reasons; first, activity during quiet inspiration was only detected by the needle electrode when it was actually in the intercostal space deep to the external oblique; second, the external oblique of this subject has been examined many times with both surface and needle electrodes and never found to contract during quiet inspiration.

This experiment, together with the evidence already reported, establishes two points: first, the intercostal muscles contract during inspiration in quiet or moderately increased breathing in many normal subjects; secondly, their activity under these circumstances can be detected by surface electrodes in

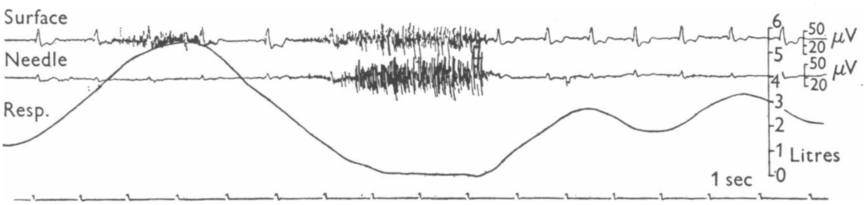

Fig. 5. Simultaneous recording with surface and needle electrodes. Maximum inspiration and expiration. All experimental conditions were the same as in the lower tracings of Fig. 4. Surface record. The activity early in inspiration probably came from the intercostals. The activity at the end of maximum inspiration and during maximum expiration probably arose predominantly in the external oblique. Needle record. There was activity early in the maximum inspiration and in the inspiratory phase of the two breaths at the end of the record. There was also marked activity during maximum expiration. All this activity probably arose in the intercostals.

lean subjects, provided the electromyogram is of adequate quality. Now, the two layers of intercostals are close together and if one of them can be detected by surface electrodes it is probable that the other can be also. It follows that the absence of activity during expiration in quiet breathing and moderately increased pulmonary ventilation (Fig. 6) means that neither intercostal muscle was contracting.

In the experiment from which Figs. 4–6 were taken, adjustments of the position of the needle produced no evidence of two layers of muscle working reciprocally. This result supports the findings with surface electrodes in all the subjects—that there was no intercostal activity during expiration in quiet or moderately increased pulmonary ventilation.

Fig. 5 is a recording from the sixth intercostal space of a maximum inspiration followed by a maximum expiration. The record taken with surface electrodes showed activity beginning early in inspiration and gradually increasing in intensity until the end of inspiration. The activity remained marked until the beginning of expiration, when it ceased, to reappear and become marked during maximum expiration. As these surface electrodes were over the external oblique muscle as well as the intercostals the activity at the end of inspiration and during expiration might be attributed to the contraction of the

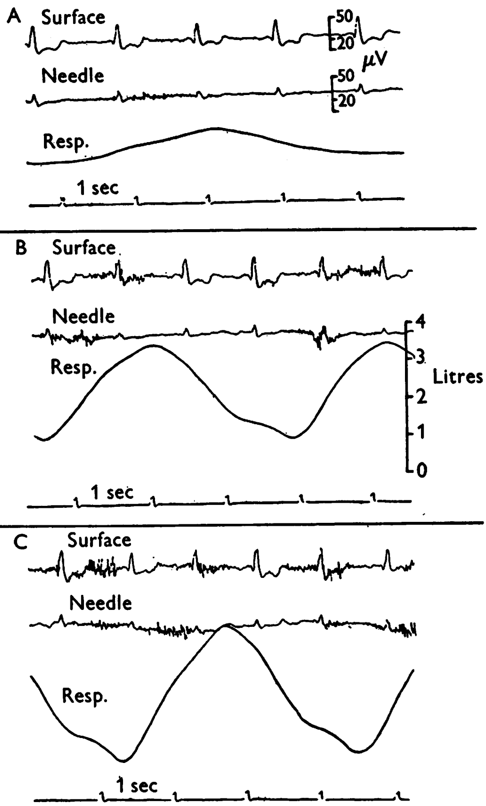

Fig. 6. Simultaneous recording with surface and needle electrodes. Increased pulmonary ventilation. All the experimental conditions were the same as in the preceding figure. The subject rebreathed expired air from the spirometer with no CO_2 absorber. A. Tidal volume 800 ml. Ventilation rate 12 l./min. Definite inspiratory activity in the intercostals detectable in both the surface and needle records. B. Tidal volume 2·5 l. Ventilation rate 45 l./min. Inspiratory activity increased in both records. C. Tidal volume 3·4 l. Ventilation rate 65 l./min. Separate bursts of inspiratory and expiratory activity in both records. All the activity in the needle record and the inspiratory activity in the surface record probably arose in the intercostals. The expiratory activity in the surface record probably arose in the external oblique.

external oblique. The activity during the early part of inspiration, however, was probably intercostal in origin for the reasons given in the analysis of Fig. 4. Activity was also seen towards the end of inspiration in the breaths which followed the maximum expiration. Contraction of the external oblique did not occur during such breaths in this subject.

The record taken with the needle electrode showed slight activity at the beginning of inspiration which ceased after about 1 l. of air intake. There was then little activity during the rest of the maximum inspiration and the early part of expiration. During maximum expiration very marked activity developed. This record presents two problems in interpretation. First, why did activity cease during the latter part of inspiration? The first possibility to be considered is that the needle had been displaced. This suggestion can be excluded for a number of reasons: the manoeuvre was repeated several times with the same result, and breaths of normal depth following maximum expiration showed inspiratory activity as before. The silence in the needle record at the end of inspiration was, therefore, probably due to cessation of activity in the motor units near the tip of the electrode. It was probably not due to relaxation of the whole intercostal muscle because, as is shown by Figs. 4 and 6, surface electrodes detect intercostal activity throughout inspirations of up to 3 l. in depth. No evidence was found in this or other experiments that the cessation of activity in late inspiration is of general occurrence. It, however, facilitated the interpretation of this particular experiment.

The second problem presented by the needle electromyogram in Fig. 5 is the origin of the marked activity during maximum expiration. It was almost certainly intercostal because there was no evidence that the needle had been displaced from the intercostal space. The view that the expiratory activity recorded by the needle electrode was due to spread from the external oblique, which was contracting forcibly, must be considered but is unlikely because the activity in the needle record was too great to be due to units more than a few mm away. Nor was the activity in the external oblique at the end of maximum inspiration detected by the needle electrode, as it would have been if the expiratory activity was due to spread from this muscle.

Fig. 6 was obtained immediately before Fig. 5. It shows the changes that occurred during progressively increasing pulmonary ventilation. A was taken immediately after the beginning of the experiment; the tidal volume was 800 ml. and the ventilation rate 12 l./min. The conditions were therefore practically those of quiet breathing. Both the surface and needle records show activity during inspiration but not during expiration. The external oblique of this subject has been examined many times and no activity was ever detected during quiet breathing in this posture. This fact, together with the evidence of Fig. 4, proves that the inspiratory activity recorded in Fig. 6 arose in the intercostal muscles.

During B the tidal volume was 2·5 l. and the ventilation rate 45 l./min. There was more intense activity in both the surface and needle records during inspiration. The activity detected by the needle, however, ceased towards the end of inspiration. This point has been discussed in the analysis of Fig. 5. The needle record showed no activity during expiration, but the surface record showed activity towards the end of expiration which probably arose in the external oblique. During C the tidal volume was 3·4 l. and the ventilation rate 65 l./min. Activity appeared in the needle record towards the end of expiration. The evidence of Fig. 5 makes it probable that this activity arose in the intercostal muscles.

On repetition of the experiment from which Fig. 6 was taken, the ventilation rates at which expiratory activity appeared in the surface record were: 37, 45, 54 and 48 l./min, and in the needle record: 38, 60, 61·5 and 63 l./min.

Summary of the findings with the needle electrode. The intercostal muscles contracted during the inspiratory phase of quiet breathing. They contracted during voluntary maximum expiration. During increased ventilation they did not contract in the expiratory phase until the ventilation rate reached 50–60 l./min.

The effects of posture

The electromyograms obtained with surface electrodes from the upper and lower intercostal spaces were compared in the supine and erect postures (Fig. 7). Four subjects were examined during quiet breathing and increased pulmonary ventilation.

No significant activity was detected in the second, third or fourth spaces of any subject in either posture.

Two subjects showed a definite increase in the inspiratory activity of the lower intercostals in the erect posture; in the other two subjects posture had no effect. Expiratory activity was not detected over the lower spaces during quiet breathing; during increased pulmonary ventilation it was always less than that recorded from the main mass of the external oblique.

DISCUSSION

For an adequate understanding of the physiology of the intercostals data of three kinds are needed: first, on the mechanical action of the muscles on the ribs; secondly, on the respiratory function of the muscles, i.e. whether they are inspiratory, expiratory or both; thirdly, on the circumstances in which they contract in the intact organism. For example, it is not justifiable to conclude that because one or other intercostal muscle when contracting in isolation raises the lower rib to which it is attached, it can, therefore, only be a muscle of inspiration. Conversely, the observation that one or other intercostal muscle contracts during inspiration in quiet breathing does not prove that the muscle is inspiratory in function (i.e. causes the intake of air into the lungs), and it does not prove that the action of the muscle is to raise the lower rib to which it is attached. It is possible that the intercostal contraction merely increases the tension of the intercostal tissues.

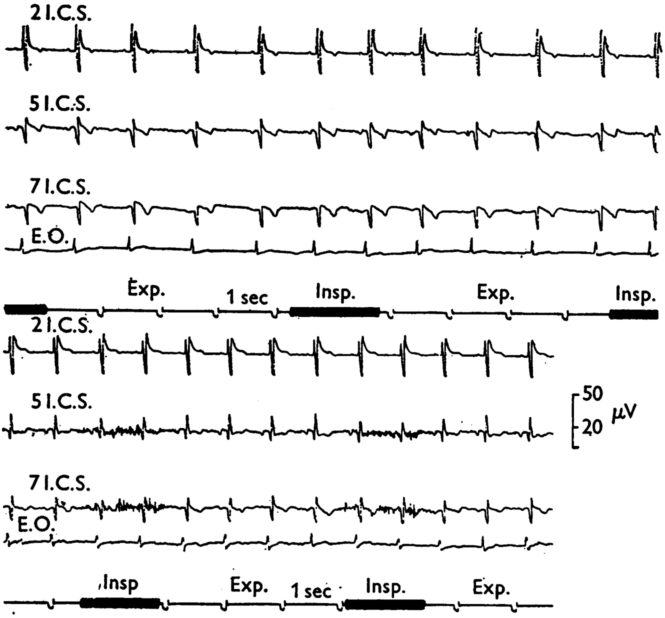

Fig. 7. The effects of posture. Records taken from the second, fifth and seventh intercostal spaces (I.C.S.) and from the external oblique (E.O.) in the abdomen. The subject breathed quietly with no respiratory apparatus. Phases of respiration were signalled by the observer. Upper tracings. Subject supine. No definite activity present at any site. Possible slight inspiratory activity in the fifth and seventh spaces. Lower tracings. Subject standing at ease. Definite inspiratory activity in the intercostals of fifth and seventh spaces. No other activity in any of the records.

The actions and functions of the intercostal muscles have been a subject of controversy throughout medical history. Beau & Maissiat (1843) listed seven distinct theories, and a review of modern standard works of anatomy shows that there is still no uniformity of teaching. The most widely held view appears to be that associated with the names of Bayle and Hamberger which maintains that the external intercostals and the interchondral portion of the internal intercostals are inspiratory in function, while the interosseous portion of the internal intercostals is expiratory. Electrical recordings from the intercostal nerves (Bronk & Ferguson, 1935) and muscles (Anderson & Lindsley, 1935) in anaesthetized cats showed that the phasic behaviour of these muscles was in accord with Hamberger's theory. Gesell (1936) examined dogs electromyographically and found that though the usual pattern was in accord with the theory there were numerous individual variations and discordant findings. Chennells (personal communication) who made many electromyographic observations on the intercostals of the cat, rabbit and rat, found that the usual pattern was in accord with the theory but exceptions were common. The non-electrophysiological studies of the last eighty years are even more equivocal and in a critical review, Campbell (1954) concluded that there was inadequate evidence from which the functions of the muscles could be deduced.

It is tempting to dismiss the intercostals as being too small and thin to be capable of any significant function, but against this view must be set the following observations.

They have a relatively good mechanical advantage about the rib axes. This observation is more significant when the poor mechanical advantage possessed by many limb muscles is remembered.

From an examination of the older German anatomical literature, Otis, Fenn & Rahn (1950) concluded that the intercostals were mechanically capable of producing very high levels of pulmonary ventilation. Fick (1923) estimated that the scaleni were potentially only one-fifth as effective respiratory muscles as the intercostals.

Duchenne (1867) obtained movements of the thoracic cage as a result of faradic stimulation of the intercostal muscles in man. He did not, however, give sufficient details of the localization of the response.

Alexander (1929), Cetrángolo (1930) and Joly & Vincent (1937) showed that destruction of all the intercostal nerves on one side (in the treatment of pulmonary tuberculosis) reduced the amplitude of the rib movements in breaths of normal depth. Lemon (1928) concluded from a thorough study of the relations between the different groups of respiratory muscles that 'there is only one procedure that consistently alters the...outward movement of the... costal margin: paralysis of the intercostal muscles on one side'.

It has been shown in the present study that during quiet breathing the intercostals contract only during inspiration. This observation taken in conjunction with the evidence of Alexander (1929), Cetrángolo (1930), Joly & Vincent (1937), is very suggestive that the intercostals are inspiratory in function during quiet breathing. I have observed inspiratory contraction of the intercostals and expansion of the lower chest in a young man with a paralysed diaphragm and whose abdominal muscles were inactive. This last finding suggests that when the intercostals act in isolation they are inspiratory in function.

There remains the possibility that the intercostals are also expiratory in function. From the findings in the present study it seems unlikely that they have any expiratory function during involuntary breathing but they probably contract strongly during voluntary expiratory efforts and in such manoeuvres as coughing. The present study has provided no evidence in support of the view that the internal and external intercostals have antagonistic actions, and the findings with the needle electrode are opposed to such a conclusion.

SUMMARY

1. The intercostal muscles were examined electromyographically using surface electrodes in healthy young men, in women after radical mastectomy, and in dyspnoeic patients. The intercostal muscles of one young man were examined simultaneously with surface and needle electrodes.

2. They were found to contract in the lower (sixth, seventh, eighth) intercostal spaces of most subjects in inspiration during quiet or slightly increased pulmonary ventilation.

3. They did not contract during expiration in quiet breathing or considerable hyperpnoea. In these circumstances they were less active than the muscles of the abdominal wall.

4. They contracted during voluntary expiratory efforts.

5. Their activity was more difficult to detect in the upper (second, third, fourth) than in the lower (sixth, seventh, eighth) intercostal spaces. This difference may have been due to any or all of the following factors: the greater depth from the surface of the skin to the muscles in the upper spaces; less activity in the intercostal muscles of the upper spaces; smaller motor units in the intercostal muscles of the upper spaces.

6. In some subjects the inspiratory contraction of the lower intercostal muscles was increased in the erect posture.

7. No data were obtained which supported the distinctions often made between the actions of the external and internal intercostals.

8. A review of the literature did not yield adequate evidence from which the functions of these muscles could be inferred with certainty. It is suggested that during involuntary breathing they are inspiratory in function, but they probably facilitate voluntary expiratory efforts and such activities as coughing.

I would like to thank Prof. Samson Wright for his guidance and advice. I am grateful to Dr A. J. H. Hewer and Dr P. H. S. Silver for help with the experiment using the needle electrode. I would like to thank Dr H. L. Marriott, Dr F. H. Scadding, Mr R. S. Handley and Mr L. P. LeQuesne for permission to study patients under their care. Finally I would like to express my gratitude to the subjects and to the technical staff of the Physiology Department for their co-operation.

REFERENCES

ALEXANDER, J. (1929). Multiple intercostal neurectomy for pulmonary tuberculosis. *Amer. Rev. Tuberc.* **20**, 637–684.

ANDERSON, F. M. & LINDSLEY, D. B. (1935). Action potentials from intercostal muscles before and after unilateral pneumectomy. *J. Lab. clin. Med.* **20**, 623–628.

BEAU, J. H. S. & MAISSIAT, J. H. (1843). Recherches sur le mécanisme des mouvements respiratoires. *Arch. gén. Méd.*, ser. 4, **1**, 265–295.

BRONK, D. W. & FERGUSON, L. K. (1935). The nervous control of intercostal respiration. *Amer. J. Physiol.* **110**, 700–707.

CAMPBELL, E. J. M. (1954). The muscular control of breathing. Ph.D. thesis, University of London.

CAMPBELL, E. J. M. & GREEN, J. H. (1953). The expiratory function of the abdominal muscles in man. An electromyographic study. *J. Physiol.* **120**, 409–418.

CETRÁNGOLO, A. A. (1930). La movilidad de la pared costal después de la neurectomia intercostal múltiple. *Rev. méd. lat.-amer.* **15**, 1224–1234.

DUCHENNE, G. B. A. (1867). *Physiologie des mouvements démontrée à l'aide de l'expérimentation électrique et de l'observation clinique, et applicable à l'étude des paralysies et des déformations*, pp. 443–503. Translated by KAPLAN, E. B. (1949). Philadelphia: Lippincott.

FICK, R. (1923). Über die Zwischenrippenmuskeln. *S.B. preuss. Akad. Wiss., Physik.–math. Kl.*, 65–72.

GESELL, R. (1936). Individuality of breathing. *Amer. J. Physiol.* **115**, 168–180.

JOLY, H. & VINCENT, PH.-A. (1937). Rôle respiratoire des muscles scalènes et inter-costaux étudié en fonction de la collapsothérapie pulmonaire. *Arch. méd.-chir. Appar. resp.* **12**, 392–404.

LEMON, W. S. (1928). The excursion of the costal margins and of the costal arch following phrenic neurectomy: experimental and clinical observations. *Minn. Med.* **11**, 675–677.

OTIS, A. B., FENN, W. O. & RAHN, H. (1950). Mechanics of breathing in man. *J. appl. Physiol.* **2**, 592–607.