

## CHAPTER VIII

# Intercostal Muscles and Diaphragm

### SPINDLES IN RESPIRATORY CONTROL

#### Introduction

The new ideas on the role of the gamma loop in motor control began to influence the study of respiration some time before anyone had taken the quite considerable trouble of recording from intercostal spindle afferents or their fusimotor neurons. Thus Nathan & Sears (1960) followed Eldred, Granit & Merton (1953) in interpreting their finding in a patient to the effect that the activity of his unilaterally deafferented intercostals was diminished by comparison with the intact side and with the status before the operation. These authors also gave a valuable review of the old literature on the effects of root section (cf. also Euler & Fritts, 1963; Sears, 1964e; Glebovskij, 1965).

Campbell & Howell (1962, 1963), from experimental work on man referred to in their papers, had come to conclusions which could be simplified as follows: in studies of respiration they had found that the effect of a resistive load in breathing through restricted orifices could be detected at a threshold of 0.6 cm H<sub>2</sub>O per litre per sec. Hence some kind of sense organ detecting the change in the relation of pressure to volume was required. Now this relation does not change across the lungs with the external load. Therefore volume is assumed to be translated into length in the intercostal muscles whose length receptors over the gamma loop are adjusted to the demanded tidal volume. With breathing hindered, the ventilatory requirements are initially unaltered. Nevertheless the respiratory effort is immediately increased in compensation. This postulate, as we shall see, was proved true by electrophysiological work (see below). In theory this happens because the demand for a given tidal volume resides in a "wanted" length in the biased spindles. The impediment to respiration prevents the wanted length-setting from being realized with the muscular force allotted to a normal breath. The spindles remain extended and therefore continue to discharge impulses which force the alpha motoneurons to increase their

firing. This drive stops when intra- and extrafusal lengths are functionally equal. The point of equality corresponds to the demanded length. Without this contribution from the spindles the alphas could not have "known" so soon that their output needed to be increased. In the end they would have augmented their activity in response to the later changes in the composition of the blood gases actuating supraspinal receptors. The theory thus explains why the correction followed without delay. It should be noted that the vagal contribution to respiratory control has been found less important in man than in the cat (Campbell & Howell).

### Intercostal Alpha-Gamma Linkage

At much the same time experimental work on the intercostal nerves was started by C. v. Euler (summaries, 1966a,b) in Stockholm and Sears (summary, 1964e) at Canberra. As a consequence of direct recording from spindle afferents (Euler and co-workers) and from efferent alpha and gamma motoneurons (Euler, Sears) our knowledge of reflex respiratory control is now in a phase of re-integration. Their results are also of great interest from a general point of view because respiration has provided opportunities of observing natural and regularly recurring rhythmic movements, well controlled and easily modifiable. Two of the recent discoveries (Critchlow & Euler, 1963; Eklund, Euler & Rutkowski, 1963, 1964; Sears, 1964b,d) may be regarded as basic for the interpretation of what has proved to be a harmonious combination of direct and indirect excitation in motor control: (i) rhythmic alpha-gamma co-activation in quiet breathing and (ii) a steady tonic discharge from the gamma motoneurons. From these two fundamental observations the analysis has developed in different directions.

Figure 94(a) presents simultaneous records of the activity in alpha and fusimotor gamma fibres in nerve twigs of an external (inspiratory) intercostal muscle; (b), removal by lignocaine of the fusimotor component; (c) is another record such as (a); (d), the same after lignocaine; (e) shows fifteen superimposed sweeps of a reflex response to stimulation of a cutaneous nerve. The record, (e), emphasizes that the fusimotor gamma neuron (in these pentobarbitone cats) has lower threshold than the alpha motoneuron. In this respect, as in their spontaneous activity varying from 4 to 140 imp/sec (Eklund *et al.*, 1964), the intercostal fusimotor gamma neurons behave like their opposite numbers in the extremities.

For an analysis of the kind described in Fig. 94, the first precaution is to sever the vagus nerves. In the cat there are several vagus reflexes from lung, bronchial, and tracheal receptors on respiration, the best

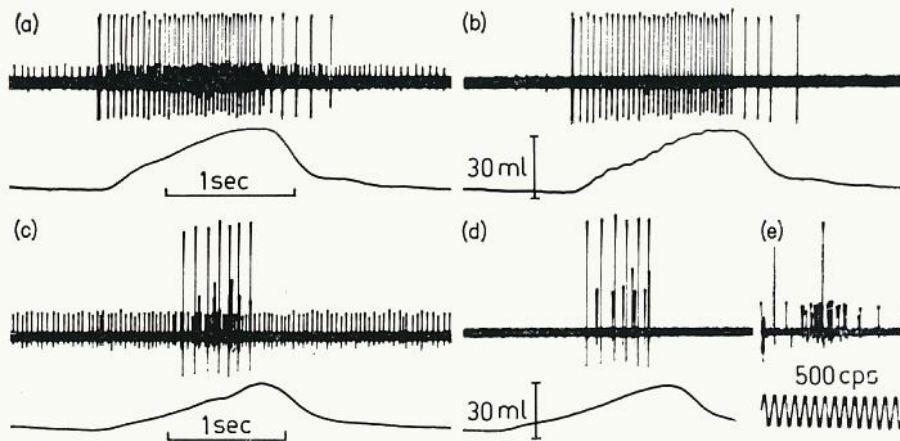


FIG. 94. Cat. Efferent inspiratory activity from two different branches ((a), (b) and (c)–(e) respectively) of the external intercostal nerves. (a) Shows one alpha and one “rhythmic” gamma fibre which was selectively blocked (b) by 0.125% lignocaine. (c) Shows three alpha and one “steady” gamma fibre (conduction velocity 25 m/sec) which was selectively blocked (d) by 0.125% lignocaine. (e) Shows fifteen superimposed sweeps of the responses to single shocks to the lateral cutaneous nerve of the same segment. Only the gamma fibre gave a reflex response. The lower tracings represent tidal volume. In this and all subsequent figures upward deflexions denote inspiration. (Eklund, Euler & Rutkowski, *J. Physiol.*, 1964).

known studied in efferent single-fibre preparations of the phrenic nerve (see for example Adrian & Bronk, 1928; Adrian, 1933; Widdicombe, 1954). These are the ones controlling frequency and duration of the inspiratory phase and elicited mainly by inflation of the lungs. Further observations have been reported by Euler & Fritts (1963) and Sears (1964c, d). Except when reflexes of the vagus were the subject of study its afferent contribution in the experiments to be reviewed was eliminated. The second precaution is to supplement efferent records with others from spindle afferents whose discharge integrate the net effect of overlapping fusimotor fibres and in addition reflect the influence of changes of extrafusal length, indirectly also of tension, in the extrafusal or main muscle to which these receptors belong.

Figure 95(a) demonstrates that the fusimotor drive of spindle primaries in alpha–gamma linkage is powerful enough to fire them to the very end of the phase of intercostal contraction. In fact relaxation which stretches the spindle produces temporary silence. As in the extremities (see Chap. VII) and in volitional contractions, the activated spindle apparently serves as a stretch receptor only in contraction and under these circumstances co-activation is so precise that the drive is cancelled simultaneously in both systems. After paralysis of the fusimotor gamma fibres by lignocaine the properties of the passive stretch receptor come to light (Fig. 95(b)).

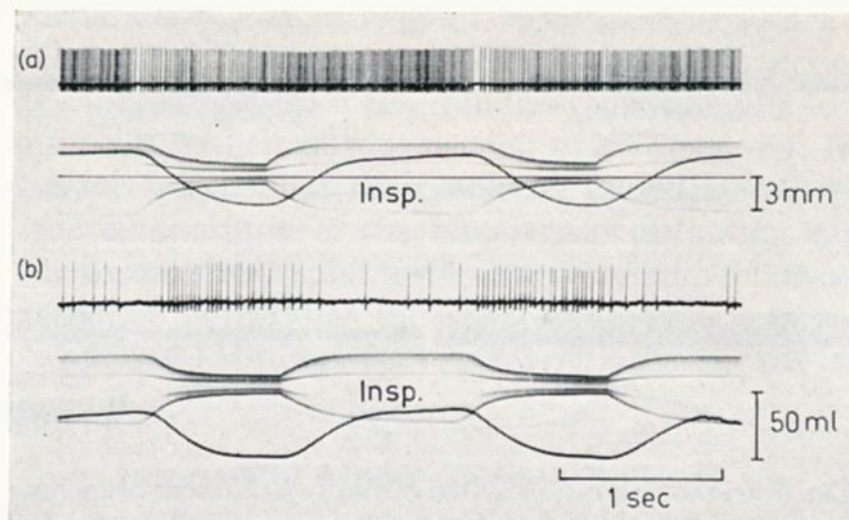


FIG. 95. Cat. Spontaneous breathing. Afferent discharge from a muscle spindle in the inspiratory muscle of the fifth interspace. (a) Control. (b) 3.2 min after application of 0.25% lignocaine solution to the intercostal nerve. Since alpha conduction still appeared unimpaired at 4.2 min after the lignocaine application the difference in discharge pattern between (a) and (b) is presumably due to the blockade of gamma motor fibres. The amplitude modulated a.c. record represents changes in intercostal width and the single trace represents tidal volume. (Critchlow & Euler, *Experientia*, 1962).

The co-activated alpha-gamma drive remains after curarization of the main muscle by Flaxedil (Eklund *et al.*, 1963), but hyperventilation stops it leaving only the tonic discharge (Eklund *et al.*, 1964; Sears, 1964b). Apparently the supraspinal instructions to alpha and fusimotor gamma neurons, as computed by the supraspinal respiratory centres, are nearly identical. The link flexibly follows changes of respiratory rate induced by vagal stimulation. Both the Canberra and the Stockholm group assume the linkage between the two systems to be spinal and Euler (1966a) has pictured it as illustrated in Fig. 96. It should be noted that internal and external intercostals are reciprocally innervated (see below).

It is possible to interfere with the instructions from the respiratory integrating centres by hindering ventilation—in animals by clamping the tracheal cannula—as explained above when discussing the experiments of Campbell & Howell on man. Critchlow & Euler (1963) and Corda, Eklund & Euler (1965a) did this and found a considerable increase in the discharge rate of inspiratory spindle primaries (Fig. 97(a)) and in the alpha output (Fig. 97(b), Fig. 98). For an electromyographic confirmation in man, see Davis, Sears, Stagg & Taylor (1965). Since no such effect could be found in the fusimotor gamma discharge, the augmented alpha output must have been a reflex to stretch produced

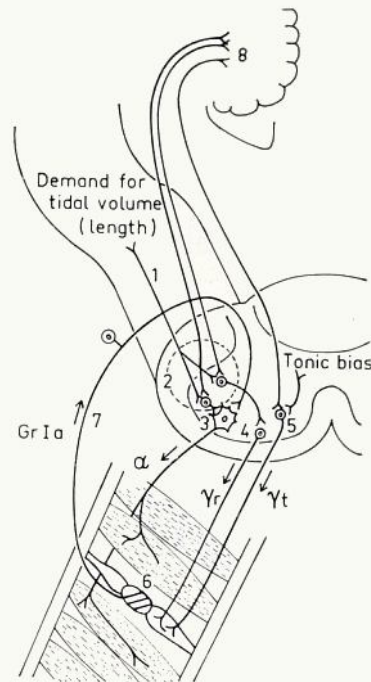


FIG. 96. Diagram to illustrate alpha-gamma linkage at the level of the spinal cord by interneurons in alpha pool (2). Commands to extra- and intrafusal musculature (6) from respiratory centres (1) and the cerebellum (8). (By courtesy of Prof. C. v. Euler).

by the increased load. (Stretch reflexes to pull on intercostal muscles have been studied by, for example, Glebovskij, 1965). This deduction was proved true by the demonstration in Fig. 98 that it was abolished by de-afferentation. Identical findings were reported by Sears (1964b) for the alpha output, found by him to have a monosynaptic component. The augmented response to tracheal occlusion was therefore called by Euler the "load compensating reflex". From the analysis given in Chap. VII it follows that such a reflex would be virtually inevitable whenever in linked alpha-gamma action there is an increase of load and hence an increased pull on the spindles.

The parallel instructions to the alpha and fusimotor gamma motoneurons need not be different. The gamma motoneurons are smaller than the alphas and hence more sensitive to the same set of instructions delivered by impulses from the supraspinal respiratory governor. The intrafusal muscular apparatus is slower than its extrafusal counterpart so that the effect of loading has time to go round the central part of the circuit and re-excite the alpha motoneurons until the point of functional equality of intra- and extrafusal length is reached, that is, when tension on the receptor endings is gone. To put it differently, the basic properties of the gamma motoneurons and their intrafusal fibres can fully

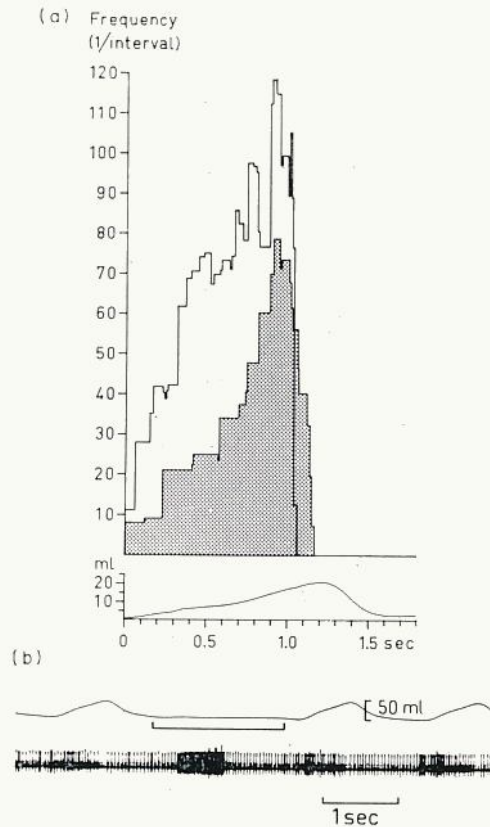


FIG. 97. Cat. (a) Discharge frequency curves of the summed efferent alpha activity in a branch of the external intercostal nerve during unrestrained spontaneous inspiration (stippled area) and during the first inspiratory effort after occlusion of the airways (in full). Below is the volume tracing of the airways given on the same time scale. (b) Afferent discharge from an external intercostal (inspiratory) muscle spindle (the larger spike) to show the response to tracheal occlusion (marked by horizontal line). Upper tracing represents tidal volume. (Corda, Eklund & Euler, *Acta physiol. scand.*, 1965).

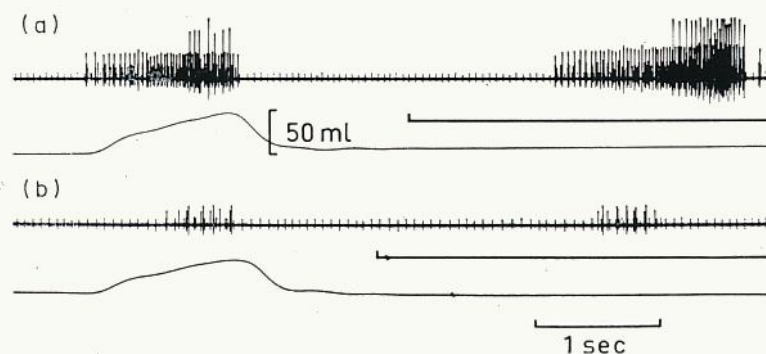


FIG. 98. Cat. Inspiratory efferent activity from a nerve branch to the external intercostal muscle to show the effect of tracheal occlusion (marked by horizontal line). Lower tracings represent tidal volume. (a) Dorsal roots intact. (b) After severing dorsal roots T4-8 ipsilaterally and T5-8 contralaterally. (Corda, Eklund & Euler, *Acta physiol. scand.*, 1965).

account for the relatively greater shortening of the intrafusal muscles in alpha-gamma linkage, deduced from the fact that in these important experiments the spindles actually do fire against contraction.

This interpretation of load compensation is the simplest possible. It is based on the experiments shown in Figs. 51 and 77 demonstrating what spindle afferents can do to motoneurons as well as what fusimotor stimulation can achieve across the loop. The interpretation assumes (Campbell & Howell, cf. above Introduction, Sears, 1964b; and Euler, 1966a, b) that the instructions to the intrafusal muscles actually embody the wanted length, demanded by the tidal volume—as such, a reasonable notion. The magnitude of the respiratory drive is likely to be adapted to the needs of the organism. The crucial question seems to be whether in normal respiration the intrafusal contraction sets the length of the main muscle and forces it to attain it, as seemed likely for the postural reflexes of the limb of the decerebrate animal which do not come off in de-afferented animals (Eldred *et al.*, 1953; Matthews & Rushworth, 1957, 1958). In rhythmic respiration, however, the alpha component cannot be abolished by root section, although it is weakened (Fig. 98 and Euler & Fritts, 1963; Sears, 1964b). In respiration it is therefore more likely that the role of the spindle is to serve as an error detector correcting misalignment between the extra- and intrafusal musculature and as an aid in the depolarization of the motoneurons. The great advantage for the motor act of depending on the indirect route over the spindle primaries for the critical amount of depolarization of its acting alpha cells lies in the ensuing automatic and rapid stabilization of the length setting (tidal volume). This happens normally as well as when breathing in the moving animal is threatened by external influences acting on the chest or the diaphragm.

In this connection the “tonic” fusimotor gamma fibres which mostly converge on the same spindle as their “rhythmic” counterparts, play a role of their own. This is well illustrated in Fig. 99 which is a graphic analysis of the tetanic and post-tetanic effects on the discharge rate of an intercostal inspiratory muscle spindle activated from a point on the contralateral side of the anterior cerebellum, an organ known from the early work of Moruzzi (1940) to influence respiration (Meulders, Massion & Colle, 1960). The hatched portion is the control, the dotted line the discharge rate during stimulation and the continuous line the post-tetanic response. The increased tonic and rhythmic discharges during cerebellar stimulation are supplanted post-tetanicly by a passive spindle response. In such experiments the tonic fusimotor gamma outflow is supposed to be responsible for the tonic effects on the spindles. A tonic fusimotor discharge was noted by Critchlow & Euler (1963) and

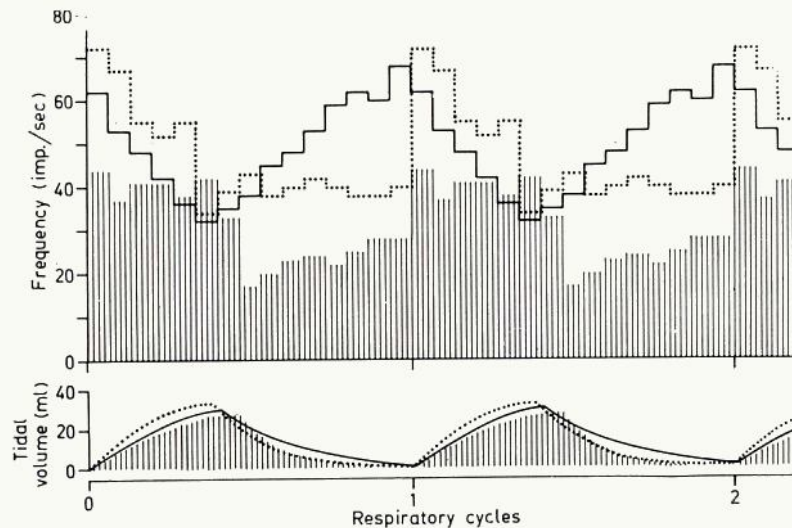


FIG. 99. Cat. To show the tetanic and post-tetanic effects on an "inspiratory" spindle of contralateral paravermian stimulation. Graphical representation of the variations in impulse frequency with respiration. Hatched diagram represents the control. Dotted line during tetanic stimulation (1.0 V; 180 shocks/sec). Continuous line is the post-tetanic frequency curve. Below are represented the corresponding tidal volumes. Note that the durations of the inspiratory phases during and after stimulation are relatively shorter than in the control diagram. (Corda, Euler & Lennerstrand, *J. Physiol.*, 1966).

studied in greater detail by Corda, Euler & Lennerstrand (1966) who added observations also on primary spindle afferents (Fig. 99).

By the experiments of Corda *et al.* (1966) it has been established that the cerebellum has also a powerful influence on the fusimotor component of intercostal control. Inspiratory and expiratory spindles are often affected in the same direction whereas reciprocity, with a relatively weaker effect on the expiratory side is characteristic of the rhythmic mechanism discussed above (Sears, 1964b). The cerebellar region responsible for these effects overlaps with the one controlling forelimb tone, as in the cerebellar effects studied by Moruzzi (1940). It generally produces contralateral excitation and ipsilateral inhibition. While it seems evident that the chest must be adapted to, and hence included in the postural regulation controlled by the cerebellum, the precise tasks of this governor in the life of the animal remain to be elucidated.

A general observation is that in many of the reflexes from the limbs (Sears, 1964b) and the skin (Sumi, 1963) on intercostal spindles, the tonic component is the only or most prominent one (Corda *et al.*, 1966), sometimes operating in the same direction as its rhythmic counterpart, sometimes independent of it. Thus lateral flexion of the head toward the recording side tends to excite both inspiratory and expiratory spindles; the opposite effect is caused by turning the head in

the opposite direction (Corda *et al.*, 1966). An effect on the spindles from passive movements of the chest wall was noted by Critchlow & Euler (1963) and found by Corda *et al.* to be exclusively concerned with tonic activity. For other reflex effects their paper should be consulted. Some of these postural reflexes have been recorded electromyographically by Meulders, Massion & Colle (1960). However, the relation between tonic spindle effects and the alpha output lacks the stringency that was found to characterize the alpha-gamma linkage tying together the activities of the rhythmic fusimotor and alpha motoneurons. These have been integrated into a specific respiratory governing system run by the so-called respiratory centres.

An attempt to summarize in outline what is known about the tonic fusimotor gamma control of the intercostal muscles would need to emphasize (i) that, when the tonic effect is strong enough, it is capable of over-riding the rhythmic effect of alpha-gamma linkage and (as in Fig. 99), make an inspiratory spindle respond as a passive stretch receptor in the expiratory phase; (ii) that tonic activation is linked with alpha reflexes of the intercostal muscles but in a less rigid manner than is the rhythmic mechanism controlled supraspinally and (iii) that tonic and rhythmic fusimotor gamma neurons converge onto the same spindle, making an effect such as, for instance, that of Fig. 99 possible. The precise circumstances under which various tonic effects on the intercostal muscles are called upon to modify respiration are unknown but have to be searched for in the adjustments of the chest in relation to changes of body posture.

#### **Primaries-Secondaries, Dynamic-Static, in Intercostal Respiration**

In order to separate primaries from secondaries in the intercostal muscles it has been necessary to resort to the indirect, but nevertheless well established, methods described in Chaps III and IV. The short distances available have made direct measurements of conduction velocities inconvenient. Euler & Peretti (1966) relied on the differential sensitivity of primaries and secondaries to vibration and partly also on the manner in which firing was resumed after the pause of the discharge during a twitch of the main muscle. As pointed out previously (Chap. III) there is a burst from the primaries at the turning point into relaxation while the secondaries simply resume the firing rate, as set by the muscle length. Andersson, Lennerstrand & Thoden (1968b) made their chief criterion of separation of primaries from secondaries the dynamic response of the former which in the secondaries is much less prominent (Chap. IV). On the basis of a study of 160 spindle afferents

Euler & Peretti could show that the majority of the spindles of the lowest vibratory sensitivity (that is, secondaries) were activated rhythmically with respiration, just as the rhythmic primaries in the previous work of Euler's group reported above. This means (see Chap. IV) that these spindles should possess static fusimotor gamma innervation, as proved to be the case. Their role in respiration, if any different from that of the primaries, is unknown. The respiratory organization of fusimotor innervation was found to differ from that of the limb muscles in that a large number of the primary endings were dominated by dynamic fusimotor gamma neurons. This would seem to give the intercostal muscles high sensitivity to changes of load.

However, Andersson *et al.* (1968b), by their mode of analysis based on triangular stretching of the muscles, could show that under dynamic stimulation many primary endings behaved like the "intermediate" types of organ that in the leg muscles were seen in some 20% of the spindles. Such spindles differ from the more common type of primary ending in that they also respond by a maintained discharge during length decrements. In this respect they behaved like secondaries and so they would be capable of following variations of muscle length in both directions. Threshold differences between primaries and secondaries were not discernible because both types of ending fired also at minimal extensions. Both, too, had higher mean values of position and velocity sensitivity than the leg spindles. Type I and Type II effects on position sensitivity were almost equally common in the intercostal endings (as in leg flexors). On the whole, spindles in leg muscles and intercostals may be said to behave in roughly the same manner.

### **Organization of the Intercostal Motor Units**

As in the limbs, the primary afferents have monosynaptic projections on the alpha motoneurons of both external and internal intercostal muscles (Eccles, Sears & Shealy, 1962; Sears, 1964c). The former are inspiratory, the latter expiratory (Bronk & Ferguson, 1934) but their opposite actions are not, as in the limbs, coupled with reciprocal excitation and inhibition from the large spindle afferents though inhibitory afferents of unknown origin and higher electrical threshold have been observed. The motoneurons are, in fact, actuated by central respiratory "drive potentials" (Sears, 1964d) characteristically phased in relation to the respiratory cycle, and not requiring proprioceptive support to occur. The central drive potentials disappear in motoneurons within segments deprived of supraspinal control by spinalization.

Essentially the central drive potentials are waxing and waning depolarizations alternating with rhythmic repolarizations supported by

inhibition. The vagal modifications of this basic process (the Hering-Breuer reflex) are well known and need not be considered here (see for example Sears, 1964d). Euler & Fritts (1963) have shown that in the cat the vagal and the spindle contributions to respiration are quantitatively of the same order when analysed in terms of pressure-volume diagrams, in man the lung reflexes appear to be less important (cf. above).

In spite of the slow firing rate of intercostal alpha motoneurons, rarely above 15/sec in quiet respiration, there is no recurrent inhibition governing them (Eklund *et al.*, 1964; Sears, 1964d), nor, for that matter, is there any in the gammas. Afterhyperpolarizations range in duration from 65 to 110 msec with a mean value around 90 msec which (cf. Chap. VI) corresponds to that of the leg flexors. Glebovskij (1961) and Andersen & Sears (1964) have found slow and fast motor units in the intercostal muscles but the ratio of their contraction times is only 1.9 as compared with 2.8 for soleus/gastrocnemius. There is no correlation between conduction velocity and contraction time, nor is duration of afterhyperpolarization related to these properties. Calibre spectra have been published by Sears (1964a).

In view of such differences in the employment of slow and fast motor units on the one hand in the limbs, on the other, in the intercostal respiratory muscles it should be emphasized that respiration is never at rest nor requires much variation of velocity and duration of contraction. It is firmly controlled by a supraspinal governor, in its turn ruled by central chemoceptors, and this basic organization is provided with an automatic volume control in the shape of a fusimotor gamma loop. The many reflexes at its disposal belong in a more special manner to the larger field of respiratory physiology which falls outside the theme of this book.

### The Diaphragm

If on the alpha side the intercostal design differs from that of the legs in some important aspects yet has a basically similar mechanism of gamma-loop control, the differentiation has gone one step further in the diaphragm. There the spindles are few, as such, as well as relative to the tendon organs, although the alpha control of the motor units is organized much as in the intercostal musculature (for references to anatomical work on spindle content in these two muscular systems, see Corda, Euler & Lennerstrand, 1965b). The fusimotor gamma fibres are so few that they do not stand out as a separate hump in the efferent fibre spectrum (cat, Gasser & Grundfest, 1939; rabbit, Fernand &

Young, 1951; dog, Landau, Akert & Roberts, 1962). The conduction velocities, 45–60 m/sec, are comparable with those of tonic motoneurons in the leg (Landau *et al.*, 1962; Yasargil, 1962), but intracellular work (Gill & Kuno, 1963a,b) has shown that they neither possess the long-lasting afterhyperpolarization nor the recurrent inhibitory control that in the tonic soleus, for instance, serves to regulate the firing rate. The duration of afterhyperpolarization is of the order of 75 msec.

The muscle fibres of the diaphragm are organized in a complex manner. They are radial in the costal and sternal portion and even decussating in the crura so that many of them are at the same time in series with some bundles and parallel with others. From the standpoint of bio-engineering this kind of organization is unsuitable for precise length control of motor units by muscle spindles and, as pointed out by Corda *et al.* (1965b), it is impossible to rely—as has been done—on the pause in contraction for the identification of spindles. Many of them will be pulled upon by muscle bundles to which they do not belong and consequently fire to both stretch and contraction. Therefore these authors identified spindle primaries by their powerful discharge to an injection of succinylcholine (Granit, Skoglund & Thesleff, 1953). The receptors which responded to tension with but little adaptation of their firing rates were classified as tendon organs. Rapidly adapting pressure receptors were also noted. By applying these criteria to single-fibre preparations from about 1465 root filaments, Corda *et al.* proceeded to make a quantitative analysis of the properties of the receptors in the diaphragm of the cat. The conclusions of Glebovskij (1962) and Yasargil (1962) that the number of proprioceptive afferents in the phrenic nerve is relatively small was confirmed. The estimates of Hinsey, Hare & Phillips (1939) to the effect that only 2% of the total or about twenty fibres of the myelinated afferents were above 5  $\mu$  in diameter corresponded well with the sum total of the three types counted by Corda *et al.*

The distribution of the proprioceptors in the diaphragm is of some interest (Corda *et al.*). The sternal portion is devoid of proprioceptors and the rapidly adapting pressure organs are fairly evenly spread over the cupola. From the *centrum tendineum* forming the roof the crural (or spinal) muscle fibres descend to insert on the lumbar vertebrae and the arcuate ligaments. This is the portion which is best provided with proprioceptors. Thus in about 750 filaments (fifteen experiments) the crura contained ten spindles and fifteen tendon organs, the nearest or dorsal quadrant had eight spindles and twelve tendon organs while the corresponding figures for the ventral quadrant were one and two.

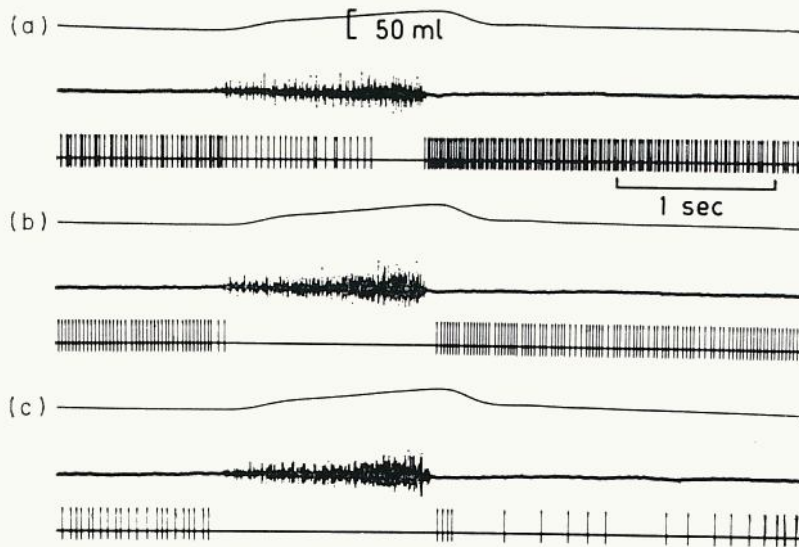


FIG. 100. Cat. Discharge from a muscle spindle of the “passive” type, located in the pars costalis of the diaphragm, and recorded from C5 dorsal root together with tidal volume (top tracing; upward deflexion denotes inspiration) and electromyogram of the diaphragm (middle tracing). Spontaneous breathing of air. (a) Control; (b) 3 min; (c) 4.5 min after application of 0.4% lignocaine solution to the phrenic nerve. Lignocaine blockade of the fusimotor fibres led to a general decrease in firing rate. Note, no effect on EMG or tidal volume. (Corda, Euler & Lennerstrand, *J. Physiol.*, 1965b).

In Fig. 100 is shown the discharge pattern of the majority of the spindles. (Primary and secondary endings were not separated.) It is of the passive type (a) in spite of some fusimotor support which disappears after lignocaine blockade of the gamma fibres (b) producing a general reduction of the spindle response. Of thirty-eight spindles only seven showed the linked, active behaviour described in the intercostals (Fig. 94) and ten signalled onset and cessation of inspiration by an increased discharge, but not its progress. The two latter types had enough fusimotor backing to increase their firing rate and maintain it when shortening of the musculature was impeded by tracheal occlusion, but the most common passive type was hardly activated by this measure which likewise failed to produce a load compensating reflex in the phrenic efferents. The only effect that could be ascribed to the fusimotor fibres was a strong increase in spindle activity to electrical stimulation of the laryngeal nerve or manipulation of the larynx which caused cough-like responses. (This description has followed that of Corda, Euler & Lennerstrand, because their analysis is more differentiated and complete than either those of Glebovskij (1962) or Yasargil (1963) though general agreement exists.)

It is evidently difficult to assign a role to the spindles in the diaphragm, beyond that of an aid in cough reflexes, as long as information

on the natural stimuli for the fusimotor gamma neurons is missing, that is, on their particular alpha-gamma linkage. Clearly the supra-spinal governors of respiration make little use of them. The alpha control appears supreme. Recently, however, some suggestive experiments by Decima, Euler & Thoden (1969) on unanaesthetized animals (decerebrates, spinal) have led to the discovery of chest-diaphragm mechanical interactions restricted to the lower intercostal spaces and emerging as reflex responses in both the phrenic and the intercostal nerves. This work may yet lead to a clarification of the role of these spindles. Their location in the crura and dorsal part of the diaphragm is also suggestive (see Decima & Euler, 1969a,b). At the moment it seems as if inhibition from the tension recorders (Gill & Kuno, 1963b) would be the most important autogenetic contribution to the regulation of the movements of the diaphragm, the pressure receptors being likely to provide information on contact with the organs in the chest (and abdomen?) above (and below?) the dome.

To the question raised at the end of Chap. VII—whether there are movements of pure alpha character—the diaphragm contractions provide a first, definite answer and so it is of some interest to consider their general characteristics. Essentially the spindle's measuring of length depends on its property of being a kind of strain gauge recording tension between fixed insertions. In the respiring diaphragm neither point of insertion is well fixed, except at one end in the crura, but even there the action of the "strain gauge" is influenced by irrelevant tensions precluding the kind of precise measuring for which these sensitive and adjustable organs are so useful. The contractions in respiration are of an isotonic type and in general the muscles which have to execute contractions of small amplitude with considerable precision (neck, pronators) are the ones provided with the greatest number of muscle spindles. For respiration, and in particular its expiratory phase, the inherent elastic forces of the system serve as a natural governor of amplitude and the intercostal volume control by the spindles adds the necessary automatic check at any required level of intake of air.