

ON THE RESPIRATORY FLOW IN THE CUTTLEFISH *SEPIA OFFICINALIS*

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Accepted 26 May 1994

Summary

The respiratory flow of water over the gills of the cuttlefish *Sepia officinalis* at rest is produced by the alternate activity of the radial muscles of the mantle and the musculature of the collar flaps; mantle circular muscle fibres are not involved. Inspiration takes place as the radial fibres contract, thinning the mantle and expanding the mantle cavity. The rise in mantle cavity pressure (up to 0.15 kPa), expelling water *via* the siphon during expiration, is brought about by inward movement of the collar flaps and (probably) mainly by elastic recoil of the mantle connective tissue network 'wound up' by radial fibre contraction during inspiration. *Sepia* also shows a second respiratory pattern, in which mantle cavity pressures during expiration are greater (up to 0.25 kPa). Here, the mantle circular fibres *are* involved, as they are during the large pressure transients (up to 10 kPa) seen during escape jetting. Active contraction of the muscles of the collar flaps is seen in all three patterns of expulsion of water from the mantle cavity, electrical activity increasing with increasing mantle cavity pressures. Respiratory expiration in the resting squid *Loligo vulgaris* is probably driven as in *Sepia*, whereas in the resting octopus *Eledone cirrhosa*, the mantle circular musculature is active during expiration. The significance of these observations is discussed.

Introduction

In the past decade, studies on the respiratory physiology of the cuttlefish *Sepia officinalis* (Johansen *et al.* 1982; Wells, 1990; Wells and Wells, 1982, 1991) have provided a good deal of information about gill morphology, oxygen extraction and blood gas transport. Wells and Wells (1982) gave the first clear account of the way in which water flows through the gills laterally and passes into the rear of the mantle cavity, thence to be expelled centrally *via* the funnel. They assumed that these inhalant and exhalant flows were the result of expansion and contraction of the mantle and stated that 'on contraction of the mantle the exhalant stream is forced forward and centrally, out through the funnel'. In this they were in agreement with Tompsett (1939), who had concluded that

Key words: cephalopods, respiration, muscles, collar flaps, mantle.

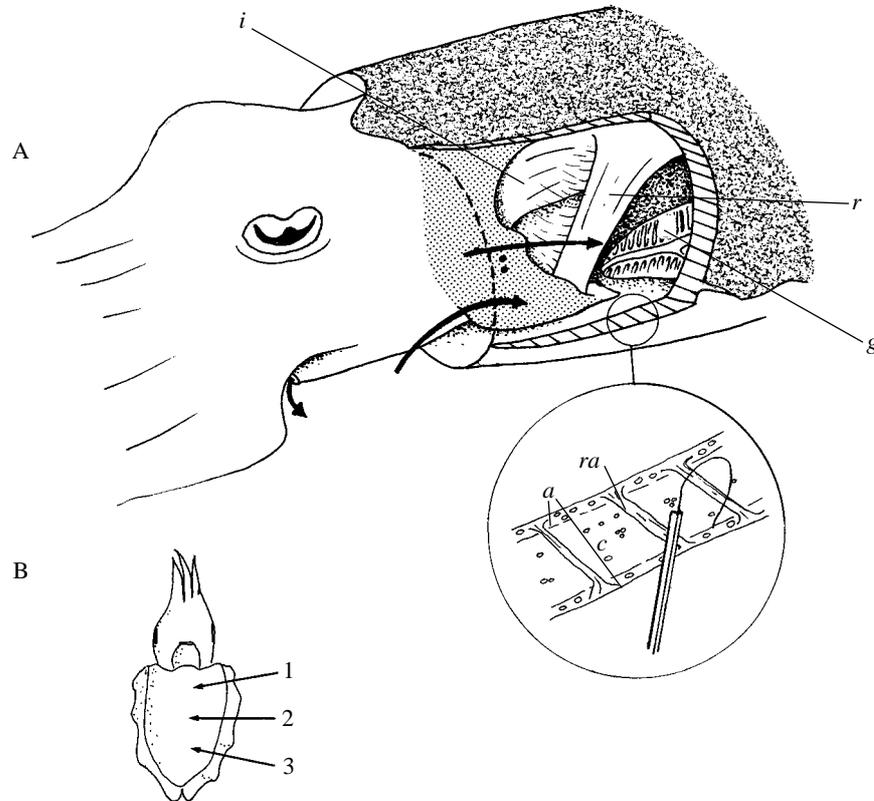


Fig. 1. Diagrams showing the arrangement of the respiratory muscles in *Sepia* and the position of the recording electrodes in the mantle. (A) Anterior region of *Sepia* with part of the mantle removed to show the collar flap (light stipple). The paired circles (●●) on the collar flap show the position of the electrodes used to record collar flap activity. Arrows indicate the entry of water to the mantle cavity, to pass over the gills (*g*). The funnel retractor muscle (*r*) joins the bottom of the collar flap near the position of the 'press-stud' (see text) and is connected by a mesentery to the edge of the inner collar muscle (*i*). The inset shows the fibre arrangement in the mantle. The thin sheets of radial fibres (*r*) separate circular fibre bundles, which consist of outer layers of 'aerobic' fibres (*ra*) and a main central mass of 'anaerobic' fibres (*c*). The position of an EMG electrode in the mantle is shown; mantle electrical activity was detected by the bared hooked tip. (B) Diagram of *Sepia* in ventral view showing the positions of the recording electrodes (1, 2 and 3).

the ventral part of the mantle was 'responsible for the continual circulation of water in and out of the mantle for normal respiration'.

Packard and Trueman (1974) monitored mantle muscle change in thickness during respiratory activity, using an impedance pneumograph and, likewise, concluded that respiratory water flow was brought about by active contractions and expansions of the anterior region of the mantle. The mantle musculature consists of bands of circular fibres, separated by thin sheets of radial fibres. Mantle contractions and reduction of mantle cavity volume result from circular muscle contraction, whilst mantle expansion results

from radial fibre contractions that make the mantle thinner and hence increase mantle cavity volume (Fig. 1). The subsequent discovery that the circular mantle muscle in *Sepia* and squid consists of a main mass of muscle composed of 'anaerobic' mitochondria-poor fibres, sandwiched between thin inner and outer layers of 'aerobic' mitochondria-rich fibres (Bone *et al.* 1981; Mommsen *et al.* 1981), led to the view that the outer 'aerobic' layers were involved in the regular rhythmic respiratory mantle movements, whilst the central 'anaerobic' zone of circular fibres operated during occasional escape jetting (see also Wells, 1988).

Curiously enough, we have now found that this apparently reasonable view is incorrect in resting animals, and that whilst the radial component of the mantle musculature in *Sepia* (consisting of mitochondria-poor fibres) is involved in *inspiration*, the mantle circular fibres are not used in *expiration* during normal resting respiration. Expiration, with a concomitant increase in mantle cavity pressure, is in fact brought about by the inward movements of the flaps formed by the collar of the funnel at the front of the mantle chamber, much as in *Nautilus* (Wells and Wells, 1985). In addition to the activity of the collar flaps during expiration, it is probable that contraction of the radial muscles during inspiration stores elastic energy in the mantle connective tissue network (the mantle 'spring') and that this is released during expiration as the mantle thickens again when the radial muscles are relaxed (see Gosline and Shadwick, 1983).

Movements of the collar flaps or valves (the outer collar muscle of Tompsett, 1939) are conspicuous during respiration, but previous workers have supposed that the movements were brought about passively by changes in water pressure within the mantle cavity rather than being actively controlled during expiration.

In other cephalopods, the situation is unclear. In both squid and octopus, there is agreement that mantle cavity expansion during inspiration involves mantle radial muscle activity, but it is still unclear how expiration is driven. In the squid *Loligo opalescens*, Gosline *et al.* (1983) made direct electromyographic (EMG) observations of mantle muscle activity during the respiration of tethered animals and observed (as we have done) two patterns of activity. The pattern involving mantle circular muscle contraction during expiration was suggested to be the normal respiratory pattern of free-swimming animals. In *Octopus*, Wells and Smith (1985) also concluded that expiration was brought about by contraction of mantle circular fibres.

Materials and methods

Our observations were made on 35 specimens of *Sepia officinalis* Lamarck, ranging from small (5 cm mantle length) to large (7.5–25.0 cm mantle length), three of *Loligo vulgaris* Lamarck (mantle length 24 cm) and two of the octopus *Eledone cirrhosa* (Lamarck) (mantle length 10–18 cm). All were trawled off Plymouth and kept in the laboratory aquarium circulation at 18 °C. The larger *Sepia* used successfully were all female, since it was found that males were less docile and much more difficult to prevent from indulging in 'spontaneous' escape jetting. After light anaesthesia with 0.2–1% ethanol, 22 gauge copper wire EMG electrodes, insulated to the tips, were inserted at different positions in the mantle and collar flap muscles (Fig. 1). The animal was then

allowed to recover (which it did within 2 min) in a small tank of sea water in a Faraday cage. The animal was not restrained, but the tank was small enough that it was only able to move 10 cm or so backwards and forwards and could not turn around. Water temperature was approximately 18.5 °C. Although once settled *Sepia* usually quietly respired in the experimental tank, precautions were required (but were not always successful) to avoid occasional escape jets dampening the apparatus and observers. A flexible polyethylene catheter attached to a Devices or a Miller pressure transducer was positioned in the mid-region of the mantle cavity. Output from the pressure transducer went to a preamplifier and thence to a 5A22N amplifier in a Tektronix 5103 oscilloscope. EMG records were made differentially between two electrodes placed 0.5–1 cm apart in the mantle or collar flap (Fig. 1). The position of the electrodes was noted before they were removed and the animals returned to the laboratory circulation. The mantle musculature in large *Sepia* is about 1.0 cm thick over most of its extent and (as shown in Fig. 1A, inset) consists of a thick central zone of mitochondria-poor circular fibres (presumably operating anaerobically) between thin inner and outer layers of mitochondria-rich fibres (presumably aerobic). Separating the bands of these circular fibres are thin sheets of mitochondria-poor radial fibres. Our EMG electrodes were placed in different positions along the mantle (Fig. 1B) and recorded from the 1–3 mm hooked tips, which were freed from insulation (Fig. 1A, inset). Thus, activity from any of the three mantle muscle components should in principle have been recorded, though which component was active could not be determined.

The electrodes led to 5A22N amplifiers in a second Tektronix 5103 oscilloscope, either directly or on-line, *via* a WPI DAM50 amplifier. From the oscilloscopes, the signals passed to a CED 1401 A/D converter and a Viglen III/25 PC, where they were collected and displayed using Chart and Sigavg programmes (Cambridge Electronic Design Ltd). They were subsequently printed on a Hewlett Packard Laserjet III printer. For comparison, similar records were obtained in the same way from the squid *Loligo vulgaris* and the octopus *Eledone cirrhosa*.

Results

Anatomy of Sepia

The siphon and collar flap musculature have previously been described and drawn by Brock (1880) and Tompsett (1939). Fig. 1A shows the arrangement schematically (with special reference to respiratory flow), as seen from an anterior-lateral view after removal of part of the mantle. Ventrally, the collar flap (light stipple in Fig. 1A) is anchored to the mantle by the 'press-stud' formed by the mantle and funnel cartilages; the large funnel retractor muscle joins the base of the collar flap at this point (Fig. 1A). Dorsally, the collar flap joins the inner collar muscle, a branch of the large head retractor muscle. The outer border (against the lateral wall of the front of the mantle cavity) is free and sweeps in and out during respiration. The flap itself is muscular; in a *Sepia* 25 cm long it is about 2 mm thick in its mid-region, thinning nearer the free border. Abbott and Bundgaard (1987) concluded from microvascular measurements that the flap muscle operated aerobically, as would be expected from its rhythmical respiratory function, but it is not known

whether two types of fibres are present (as they are in the funnel flaps of *Nautilus*, Hochachka *et al.* 1978). Since the inner border of the funnel retractor muscle is linked to the outer surface of the inner collar muscle by a sheet of mesentery, water entering the mantle cavity past the free outer border of the collar flap passes over the gills to the hind region of the mantle cavity in the way that Wells and Wells (1982) described.

Entry of water to the mantle cavity *via* the siphon is prevented by the collapse of the siphon tip during inspiration. During expiration, the collar flap seals the gap between the outer edge and the lateral border of the mantle. Escape of water between the inner ventral border of the siphon (between the 'press-studs') and the mantle edge is prevented by the ventral border of the siphon acting as a valve. Thus, water exits from the mantle cavity entirely *via* the siphon.

Respiratory rhythm

In *Sepia* at rest, the respiratory rates are between 0.8 and 1.0 Hz, and mantle cavity pressures are between 0.005 and 0.15 kPa (Fig. 2). During slow swimming, the respiratory rate is unchanged, but mantle cavity pressures increase and now range from 0.1 to 1 kPa (Fig. 3, left). During escape jetting, mantle cavity pressures greatly exceed these values, (Fig. 3, middle) rising to maxima around 10 kPa in the largest individual studied.

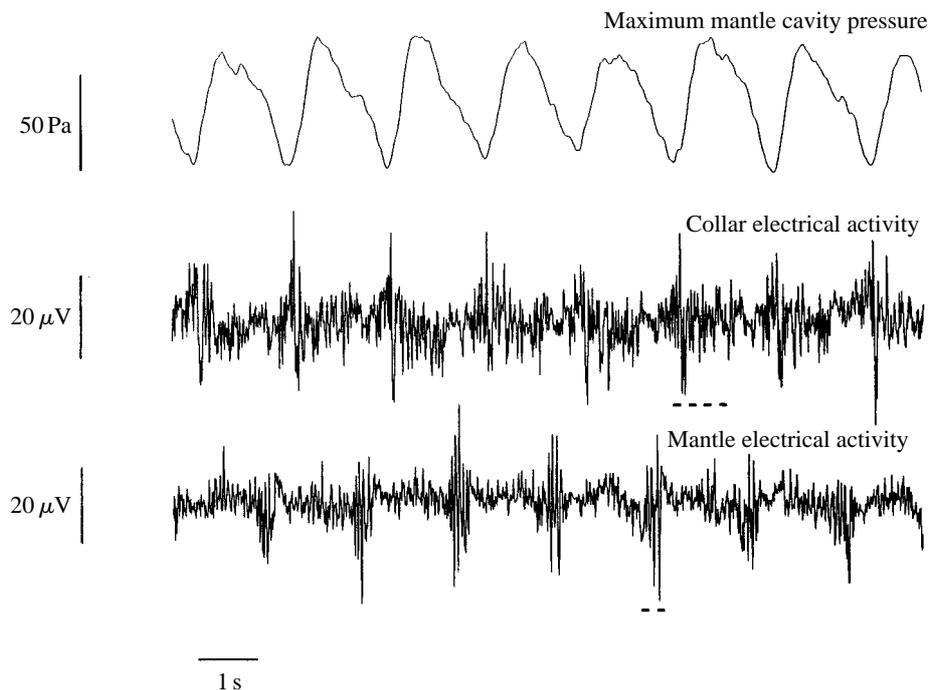


Fig. 2. Resting respiration in *Sepia* at 18°C. Note the alternation of electrical activity from collar flap and mantle, mantle activity terminating before the pressure rise at the beginning of expiration. The dotted lines under portions of the mantle and collar traces indicate the duration of activity during one respiratory cycle. Note also the low maximum mantle cavity pressure (approximately 50 Pa). Mantle recordings were taken from position 1 (see Fig. 1B).

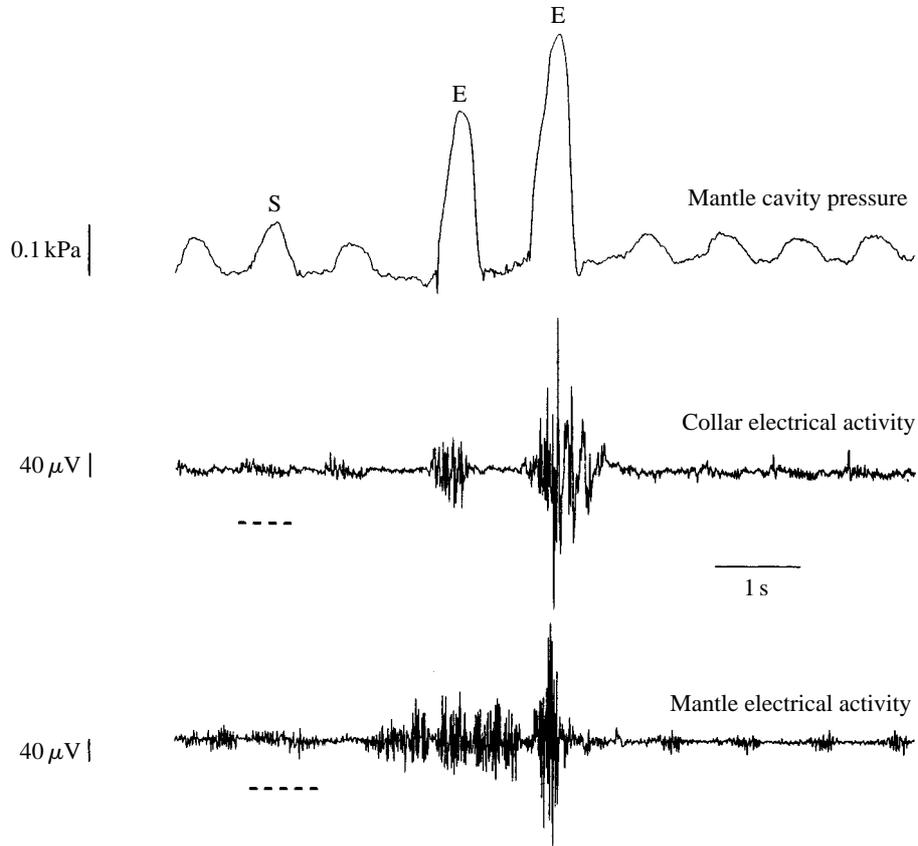


Fig. 3. *Sepia*. This record shows (left) slow swimming/deeper respiration; (middle) escape jetting; and (right) normal resting respiration. During swimming (S) the amplitude and duration of activity from both collar flap and mantle musculature is greater than during resting respiration (last three cycles of record), as are the maximum mantle cavity pressures. The two escape jets (E) in response to light mechanical stimulation show a much greater amplitude of electrical activity and very much larger pressure pulses. Note how the collar flap is electrically silent between the two large pressure transients. The dotted lines under portions of the traces of electrical activity from collar flap and mantle show the duration of activity during the swimming response. Mantle recordings from position 1, pressure traces as previously.

The pattern of the respiratory pressure pulses changes if the animal is suddenly illuminated, and their amplitude increases slightly. At other times, the animal is capable of arresting the respiratory rhythm for short periods. During resting respiration, however, the respiratory rhythm is regular (Fig. 2) and the rhythmic respiratory movements of the funnel flap muscles are visible and correlate with the pressure changes in the mantle cavity, inward movement of the flaps occurring during expiration when pressure rises and there is no swimming movement. As they sweep inwards, the resistance they meet due to the increase in mantle cavity pressure causes the inner attached portion of the flaps to bulge outwards (anteriorly). Although mantle cavity volume evidently changes during the

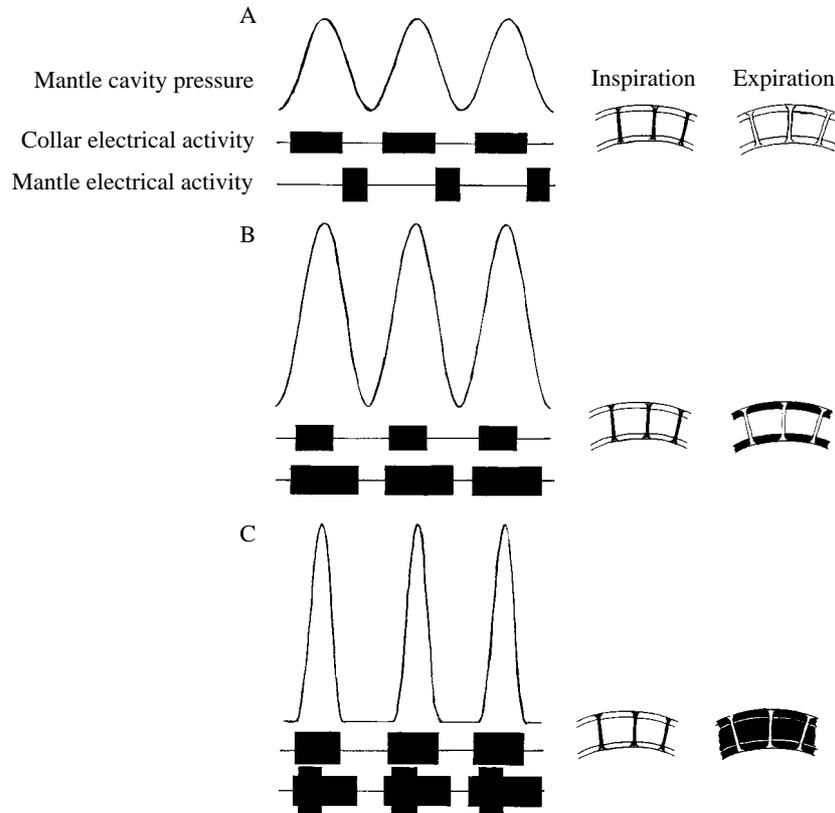


Fig. 4. Summary diagram showing phase relationships of the mantle cavity pressure to the electrical activity of the mantle and collar flap musculature during resting respiration (A), deeper respiration/slow swimming (B) and escape jetting (C). The inferred active components of the mantle musculature in each pattern are shown on the right of the figure. The 'pressure' traces do not fully represent the complex waveforms of the pressure pulses generated by mantle activity. In this diagram, and in the records of Figs 2, 3, 5 and 6, upward excursions of the pressure trace represent increases in mantle cavity pressure.

respiratory cycle, the changes are relatively small and very little dorso-ventral mantle movement is seen in side view.

Electrical activity of respiratory muscles

Three different patterns of electrical activity, which correlated with different maximum mantle cavity pressures, were observed in our EMG records from the mid-region of the collar flaps and mantle. These three patterns are seen in Figs 2 and 3 and are shown schematically in Fig. 4.

Resting respiration

In this pattern (Fig. 2 and the latter part of the record in Fig. 3), collar flap activity

coincides with the rising phase of mantle cavity pressure, i.e. the collar flap is active during expiration. Mantle activity begins as mantle cavity pressure begins to fall and ceases before pressure rises on the next expiration. It seems clear that mantle muscle activity here is solely from radial fibres, contracting to expand the mantle during inspiration. There is no mantle activity during any part of the expiratory phase. These phases of collar and mantle activity are shown schematically in Fig. 4A.

Deeper respiratory rhythm with swimming movements superimposed

In this pattern (Fig. 3, left), the electrical activity from both the collar flap and the mantle is more prolonged than in the preceding pattern. Collar flap activity occurs, as before, during the pressure rise in the mantle cavity, but it continues past the pressure peak, during the initial part of the inspiratory phase. Presumably the collar flap is actively held towards the inner collar muscles at the beginning of inspiration, to give a wider gap between its edge and the lateral part of the mantle, so as to permit easier entry of the larger volume of water respired during this pattern of respiration. The electrical activity of the mantle is of greater amplitude than in the first pattern and begins on the inspiratory phase, as before. However, it is prolonged into the beginning of the expiratory phase as mantle cavity pressure begins to rise. This extra later 'segment' of mantle electrical activity cannot be due to radial muscle activity (which can only result in reducing mantle cavity pressure) and must therefore be due to circular muscle activity. These phases of collar and mantle activity are shown schematically in Fig. 4B.

In the small tank in which our experiments were carried out, the *Sepia* were restricted in their movements, but it seems probable that, in larger tanks, this pattern represents respiration during more continuous slow swimming, when swimming movements by the fins are to some extent supplemented by respiratory expirations. Hence, it seems possible that the circular muscle activity in this respiratory/swimming pattern comes from the thin mantle layers of aerobic fibres.

Escape jetting

During escape jetting, much larger mantle cavity pressures are produced (Fig. 3, middle) and can rise transiently to around 10 kPa. During these large pressure transients, electrical activity from both collar flap and mantle is of much greater amplitude than that found during resting respiration and slow swimming. Apart from an increase in amplitude, collar flap activity is similar to that in the second pattern, occurring during expiration and during the first phases of inspiration. In contrast to the phases of activity in the collar, mantle activity is clearly divided into lower-amplitude activity during inspiration (as in resting respiration and swimming) and large-amplitude activity during expiration. The first of these mantle activity phases is presumed to be the result of radial muscle activity and the second of circular muscle activity, probably a combination of activity from the central 'anaerobic' mass of circular fibres and the outer layers of 'aerobic' fibres. These phases of collar and mantle activity are shown schematically in Fig. 4C.

Although, in principle, the electrodes placed in the mantle could record activity from all three types of mantle muscle fibre (and almost certainly did so), we can only definitely

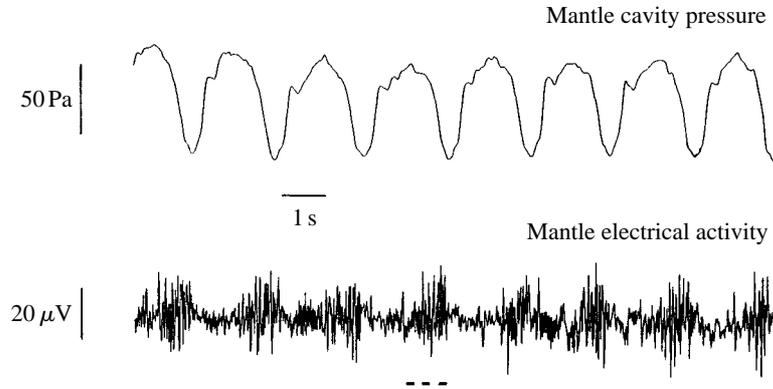


Fig. 5. Resting respiratory activity from mantle in *Loligo*. As in Fig. 2 from *Sepia*, note mantle activity during the inspiratory phase. The mantle recording was taken from a position equivalent to position 1 in *Sepia*.

distinguish between circular and radial fibres (from the phase relationship of their activity to the pressure records) and cannot distinguish between the two types of circular fibre. The large increase in amplitude between circular fibre activity during deeper respiration/slow swimming and during escape jetting suggests that in the former only the aerobic fibres are active, whilst in the latter the central anaerobic fibres are active, as shown schematically in Fig. 4B,C.

Loligo and *Eledone*

We have made fewer observations on *Loligo* and *Eledone* than upon *Sepia*. In *Loligo*, we were unable to record from the collar flaps, but activity from the mantle is only seen during inspiration, and the mantle is silent during expiration (Fig. 5), so that it seems that expiration during resting respiration is driven by the collar flaps, as in *Sepia*. During jetting (not shown), mantle circular fibres *are* active.

In *Eledone*, mantle activity alternates with the activity of the collar flaps (Fig. 6) and, as in deeper respiration in *Sepia*, collar flap activity occurs not only during expiration but also during the initial stages of inspiration as mantle cavity pressure falls. In contrast to *Sepia* and *Loligo*, however, although low-level mantle activity begins towards the end of the fall in mantle cavity pressure, it continues at higher amplitude as mantle cavity pressure rises. The mantle musculature in *Eledone* is more complex and less regularly arranged than in *Sepia* or *Loligo* (see Wells, 1988) and, in our records, although it is clear that the collar flap musculature activity is active during expiration and during the initial phase of inspiration, it is probable that contraction of the mantle 'circular' fibres is also involved in the initial phase of expiration in *Eledone*.

Discussion

Our observations indicate that at rest, *Sepia* produces the water flow over the gills with

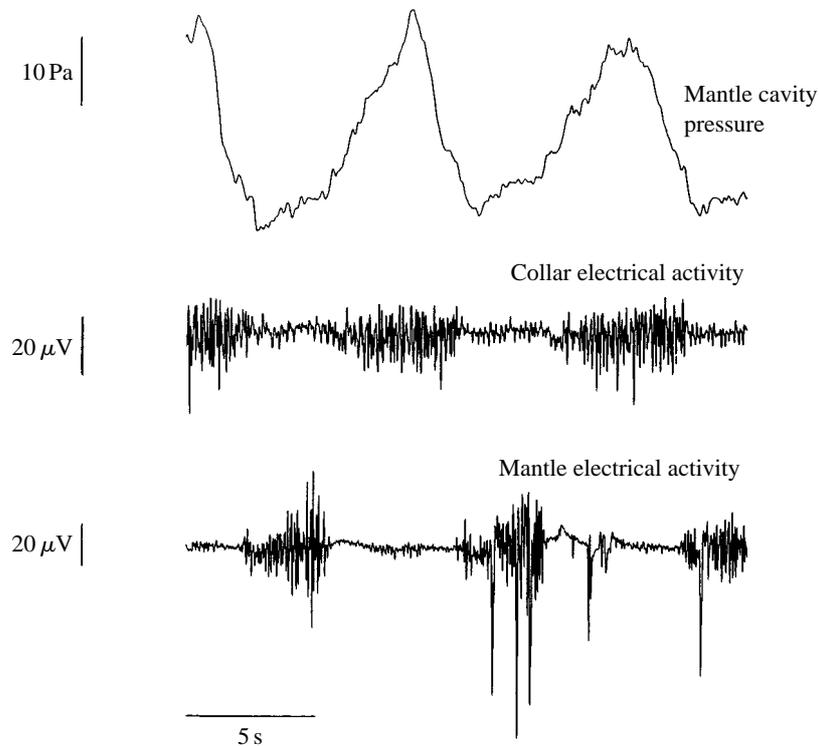


Fig. 6. Resting respiratory activity in *Eledone*. Note that mantle activity occurs not only during inspiration, but also during the slowly rising phase of expiration.

the collar flaps and with the radial component of the mantle musculature. Expansion of the mantle cavity during inspiration results from radial muscle activity thinning the mantle and some movement of the collar flaps. Expiration, involving a rise in mantle cavity pressure, is brought about by the inward movement of the collar flaps and elastic recoil of the mantle connective tissue network, following the thinning by radial muscle activity during the preceding inspiration. Mantle circular muscles are inactive during expiration. In our experiments, two types of respiratory activity were observed (each showing different patterns of collar and mantle muscle activity): resting respiration, when forward movement of the collar flaps was apparently passive, and 'deeper' respiration, when the collar flaps were moved forwards actively during inspiration and when circular mantle muscle fibres were involved in expiration. Together with escape jetting, there are thus three patterns of 'respiratory' muscle activity. In resting *Loligo* the situation is apparently the same as in resting *Sepia*, whilst in resting *Eledone*, there is some mantle 'circular' muscle activity at the beginning of expiration.

Respiratory frequency and amplitude

Our values for respiratory frequency (0.8–1 Hz) and mantle cavity pressures (0.05–10 kPa) in *Sepia* are similar to those reported by previous authors. Bert (1867)

observed values around 0.9 Hz in *Sepia* at rest. Packard and Trueman (1974) found a rather slower rate, between 0.4 and 0.6 Hz, whilst Wells and Wells (1991), using smaller animals than ours, observed rates between 1.5 and 2.0 Hz. Peak pressures within the mantle cavity during respiration are in accord with those of Wells and Wells (1991), who obtained values between 0.06 and 0.17 kPa. During escape jetting, mantle cavity pressures greatly exceed these values, rising to maxima of around 10 kPa in the largest individual studied (range 0.5–10 kPa). Packard and Trueman (1974) observed a maximum value of 9 kPa.

Nervous control of respiration

The network of lobes, or the respiratory centre, in the cephalopod nervous system that generates the regular pattern of resting respiration has not been identified. In *Octopus vulgaris*, it has been suggested that the median basal lobe (MBL) is responsible for integrating a variety of sensory inputs (optic, static, olfactory and tactile) and controlling the movements of the siphon and mantle during respiration, swimming and escape (Young, 1971). The MBL also receives a major input from the peduncle lobe which, if lesioned, evokes 'deep respiration' (Klemensiewicz, 1878; cited in Young, 1971). As the peduncle lobe is conspicuously absent in *Nautilus* (Messenger, 1970; cited in Young, 1971), where respiration is driven solely by the collar and funnel, it seems possible that the peduncle/MBL complex is involved in coordinating the mantle-mediated respiration described here, with input from the peduncle lobe modifying the motor output of the MBL (Messenger, 1967). Motor output from the MBL impinges on the palliovisceral lobe, where the collar and pallial nerves arise (Young, 1971), and Gray (1960) observed units in the pallial nerve of *Octopus* which were active during both phases of the respiratory cycle. Since mantle circular muscle fibres apparently play no role in resting respiration in *Sepia* and *Loligo*, it would be interesting to examine the pallial nerve outputs of these animals.

The respiratory muscles

Our experiments indicate that the division of the circular mantle musculature into inner and outer 'aerobic' layers and a central 'anaerobic' layer is unconnected with resting respiratory activity. It seems probable, rather, that the muscle arrangement in the mantle exactly parallels the division of the locomotor myotomal musculature of fishes into aerobic fibres used during cruising and anaerobic fibres used during bursts of rapid swimming; this would be yet another instance of the convergence of fish and cephalopods admirably discussed by Packard (1972). Wells and Wells (1991) point out that *Sepia* resembles octopods in its respiratory physiology, since both are much more efficient than squid in extracting oxygen from the respiratory flow, which in *Sepia* is of much smaller volume than in squid. Nevertheless, despite these differences in oxygen uptake and volume of water respired, the same muscle systems are employed for gill ventilation in both.

It was unexpected that the radial muscles used in inspiration are of the mitochondria-poor type (Bone *et al.* 1981), but this may reflect the requirement for maximum cross-sectional myofibril content (i.e. maximal force generation) in muscles consisting of thin

strips of fibres. It is not yet known whether the two types of mantle circular fibre (differing in mitochondrial content) are different in contraction velocity. In *Loligo*, and in the smaller squid *Alloteuthis*, the normal slow alternating backwards and forwards swimming is driven by fin movements rather than by slow jetting; hence, the rhythmic contractions of the collar flaps are required to drive expiration.

In the curious oegopsid cranchid squids, which store ammonia in the enlarged coelom to achieve neutral buoyancy (Denton *et al.* 1958), mantle contractions are not involved in respiration and, instead, water flow over the gills is driven by movements of the coelomic wall (Clarke, 1962). In *Nautilus*, where the shell would prevent mantle movements (the mantle is not muscular), the respiratory flow results from movements of the fused collar and funnel folds alone (Wells and Wells, 1985).

It seems that water flow over cephalopod gills results from rather labile mechanisms, and that particular cephalopods employ different muscular systems according to their particular mode of life and, indeed, according to circumstance. *Sepia* buries itself in the sand during the day, hiding to ambush its prey, and the collar flap system seems likely to be more suitable than the use of the mantle in passing water over the gills. The early cephalopods resembled *Nautilus* in having chambered shells and were thus unable to use the mantle for expiration (Wells, 1988) and must have used a collar-flap system. The use of the collar flaps for expiration in *Sepia*, *Loligo* and (to some extent) in *Eledone* indicates the success of this original cephalopod respiratory design. It is noteworthy that it is used both in those cephalopods (like *Sepia*) that minimise ventilation volume and extract oxygen from it efficiently and probably also in those (like *Loligo*) that extract less oxygen from a much larger volume throughput (see Wells, 1990). It would be interesting to examine expiration in highly active squids such as the ommastrephids.

We thank Professor E. R. Trueman for the loan of the Miller pressure transducer, Professor E. J. Denton for the loan of the Devices pressure transducer, and the master and crew of RV *Squilla* for the supply of animals. Dr R. Williamson kindly assisted with some experiments on *Eledone*. We are also indebted to Dr M. J. Wells for his helpful comments on experimental design and on the first draft of this paper. This work was carried out during the tenure of a Leverhulme Trust Emeritus fellowship and an Honorary MBA fellowship by Q.B., which are gratefully acknowledged, and a Wellcome Trust post-doctoral research assistantship by E.R.B. G.T. was supported by a Royal Society grant to Dr N. J. Abbott.

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