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# Gradients of strain and strain rate in the hollow muscular organs of soft-bodied animals

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The cylindrical shape of soft-bodied invertebrates is well suited to functions in skeletal support and locomotion, but may result in a previously unrecognized cost—large non-uniformities in muscle strain and strain rate among the circular muscle fibres of the body wall. We investigated such gradients of strain and strain rate in the mantle of eight long-finned squid *Doryteuthis pealeii* and two oval squid *Sepioteuthis lessoniana*. Transmural gradients of circumferential strain were present during all jets ( $n = 312$ ); i.e. for a given change in the circumference of the outer surface of the mantle, the inner surface experienced a greater proportional change. The magnitude of the difference increased with the amplitude of the mantle movement, with circular muscle fibres at the inner surface of the mantle experiencing a total range of strains up to 1.45 times greater than fibres at the outer surface during vigorous jets. Differences in strain rate between the circular fibres near the inner versus the outer surface of the mantle were also present in all jets, with the greatest differences occurring during vigorous jetting. The transmural gradients of circumferential strain and strain rate we describe probably apply not only to squids and other coleoid cephalopods, but also to diverse soft-bodied invertebrates with hollow cylindrical or conical bodies and muscular organs.

**Keywords:** strain; strain rate; cephalopod; muscle; jet locomotion; mantle

## 1. INTRODUCTION

The hollow, cylindrical shape of the bodies and muscular organs of soft-bodied invertebrates is well suited to functions in skeletal support and locomotion (e.g. Trueman 1975). This ubiquitous shape, however, may result in a previously unrecognized cost—large non-uniformities in strain among the circumferential (i.e. circular) muscle fibres of the body wall. We predict that non-uniformities in strain arise as follows (see the electronic supplementary material for a model). When the circular muscle fibres in the body wall shorten, the cylindrical body decreases in diameter, and if both the volume of tissue and length of the body are essentially

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constant, the thickness of the muscular wall increases. As the body contracts, we predict that the circular fibres near the inner lumen surface experience greater shortening than fibres near the outer surface, thereby resulting in a transmural gradient of strain (figure 1*a*). Because the fibres near the inner surface shorten a greater amount during the same time interval as the fibres near the outer surface, the inner circular fibres must shorten at a higher velocity. Thus, we predict that a transmural gradient of strain is accompanied by a gradient of strain rate.

Transmural gradients of strain and strain rate are probably important players in the evolution of musculoskeletal structure and function in hollow cylindrical organs and body walls because they may (i) require the circular fibres near the inner lumen surface to operate along different regions of the length–tension and force–velocity curves than fibres near the outer surface, and (ii) create challenges for ‘tuning’ connective tissue organization and mechanics to body wall kinematics (e.g. Thompson & Kier 2001). We investigated gradients of strain and strain rate in the mantles of long-finned squid *Doryteuthis* (formerly *Loligo*) *pealeii* and oval squid *Sepioteuthis lessoniana* using sonomicrometry, with the goal being to test the hypothesis that such gradients occur during locomotion in these soft-bodied invertebrates.

## 2. MATERIAL AND METHODS

We anaesthetized squid in cold sea water (Bower *et al.* 1999) and surgically affixed sonomicrometry transducers to the mantle (see the electronic supplementary material). The transducers were attached along the dorsal and ventral midlines within a single transverse plane that was about one-third of the dorsal mantle length from the anterior edge of the mantle, and their configuration permitted simultaneous measurements of mantle diameter and mantle wall thickness. The transducers on the outer surface of the mantle were attached with a shallow stitch of 7/0 polypropylene suture material, while one transducer was glued to the inner lumen surface of the mantle with a drop of Vetbond (3M, St Paul, MN, USA). All of the leads were secured near the collar of the squid with an additional suture to minimize their interference with swimming.

Following surgery, the squid was transferred to a shallow tank ( $2 \times 1 \times 0.15$  m deep) filled with natural sea water at  $15$ – $17^\circ\text{C}$ . Each animal recovered and then swam at various speeds using combinations of jetting and fin movements (see the electronic supplementary material). During swimming, the output from the sonomicrometer (Triton Technology, San Diego, CA, USA) was digitized and recorded at 1000 Hz. At the end of the swimming trial, we euthanized each squid by over-anaesthetizing it in aqueous magnesium chloride (Messinger *et al.* 1985) and evaluated the alignment of the transducers.

The transducers simultaneously recorded changes along the dorsoventral midline in the diameter of the outer surface of the mantle and the accompanying changes in mantle wall thickness. From these records (figure 1*b*), we then calculated circumferential strain (figure 1*c*) at the outer ( $\epsilon_{\text{OUT}}$ ) surface of the mantle as

$$\epsilon_{\text{OUT}} = \frac{(D_I - D_{\text{REST}})}{D_{\text{REST}}}, \quad (2.1)$$

where  $D_I$  is the instantaneous mantle diameter and  $D_{\text{REST}}$  is the diameter of the mantle at ‘rest’. The mantle is highly dynamic and determination of the true resting diameter or circumference is difficult. Thus, we considered the maximum diameter during low-amplitude ventilatory jets (figure 1*b*) to be  $D_{\text{REST}}$ . We next calculated circumferential strain (figure 1*c*) at the inner ( $\epsilon_{\text{IN}}$ ) surface of the mantle as

$$\epsilon_{\text{IN}} = \frac{(D_I - 2W_I) - (D_{\text{REST}} - 2W_{\text{REST}})}{D_{\text{REST}} - 2W_{\text{REST}}}, \quad (2.2)$$

where  $W_I$  was the instantaneous mantle wall thickness and  $W_{\text{REST}}$  was the mantle wall thickness at  $D_{\text{REST}}$ . We calculated strain rate by dividing the change in  $\epsilon_{\text{IN}}$  or  $\epsilon_{\text{OUT}}$  during the exhalant phase of the jet by the duration of the exhalant phase of the jet.

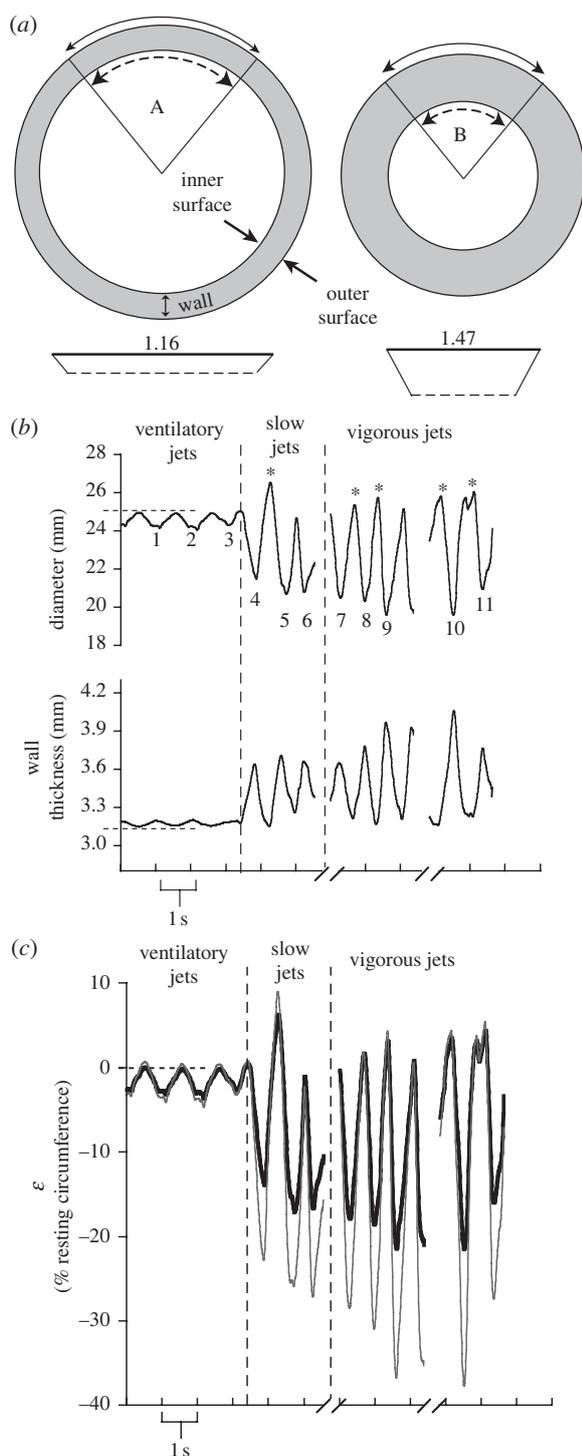


Figure 1. (a) Schematic illustrating the relative lengths of the outer and inner surfaces of the mantle prior to contraction (A, ratio = 1.16) and after a 30% decrease in the circumference of the outer surface (B, ratio = 1.47). The inner surface of the mantle experiences a proportionally greater change in length. (b) Sonomicrometry data showing mantle diameter and wall thickness changes during a series of jets: 1–3; low-amplitude, ventilatory mantle movements; 4–6; slow; 7–11; vigorous. The horizontal dashed lines near jets 1 and 2 indicate resting mantle diameter and wall thickness. The asterisks indicate hyperinflation (i.e. expansion of the mantle beyond resting diameter). (c) Calculation of circumferential strain ( $\epsilon$ ) at the outer (black) and inner (grey) surfaces of the mantle during the jets in figure 1b. Strain was calculated by equations (2.1) and (2.2) (§2). The negative signs signify a decrease in circumference relative to an arbitrary resting length (dashed horizontal line; §2).

### 3. RESULTS

A transmural gradient of circumferential strain was present during all jets in both species; i.e. for a given change in the circumference of the outer surface of the mantle, the inner surface experienced a greater proportional change (figure 2). Furthermore, the magnitude of the difference increased with the amplitude of the mantle contraction or hyperinflation (figure 2a,c). There were remarkably high strains during jetting, particularly for the circular fibres near the inner surface of the mantle, with these fibres experiencing strains of  $-30$  to  $-42$  per cent during vigorous jets. If the elongation of the circular fibres during hyperinflation is included (e.g.  $+25\%$ ; figure 2a), then the total range of circumferential strain ( $+25\%$  to  $-42\%$ ) during a single jet is noteworthy relative to vertebrate skeletal fibres, especially for muscle fibres that provide power for locomotion (Burkholder & Lieber 2001). Furthermore, the difference in strain between the inner and outer surfaces of the mantle was substantial, with fibres at the inner lumen surface experiencing a total range of strains up to 1.45 times greater during vigorous jets (figure 2c). In all jets, the circumferential strain rate was greater for the circular fibres near the inner lumen surface of the mantle than for those at the outer surface, and the magnitude of the difference increased with the amplitude of the jet (figure 2b,d).

### 4. DISCUSSION

Our results show for two species of squids that substantial gradients of circumferential strain and strain rate exist across the mantle wall. Although we do not yet understand the implication of gradients for locomotor performance of squids, such large gradients of strain and strain rate have implications for circular muscle performance. A gradient of strain (figures 1c and 2a,c) probably results in the circular muscle fibres near the inner and outer surfaces of the mantle operating over different ranges of sarcomere length and, therefore, potentially producing different levels of force during the same mantle contraction. Because the work produced by a muscle depends on the product of force and the change in length of the fibre (e.g. Josephson 1999), the unit work output may vary transmurally, particularly during the high circumferential strains of rapid jetting. Furthermore, the circular muscle fibres near the inner surface of the mantle experienced strain rates from 0.2 to 0.9 lengths  $s^{-1}$  higher than those near the outer surface during vigorous jets (figure 2b,d). These differences are large relative to the maximum unloaded shortening velocity of the circular fibres (5.1 lengths  $s^{-1}$ ; Thompson *et al.* 2008) and suggest that fibres near the inner surface experience lower loads for a given mantle contraction.

Gradients of strain require the circular fibres near the inner lumen surface of the mantle to generate force over an especially wide range of lengths ( $+25\%$  to  $-42\%$ ; figure 2a). Such performance requirements are unusual among muscles that generate power for locomotion (Burkholder & Lieber 2001), although the pectoralis fibres of pigeons come close in their operating length range ( $+15\%$  to  $-27\%$ ;

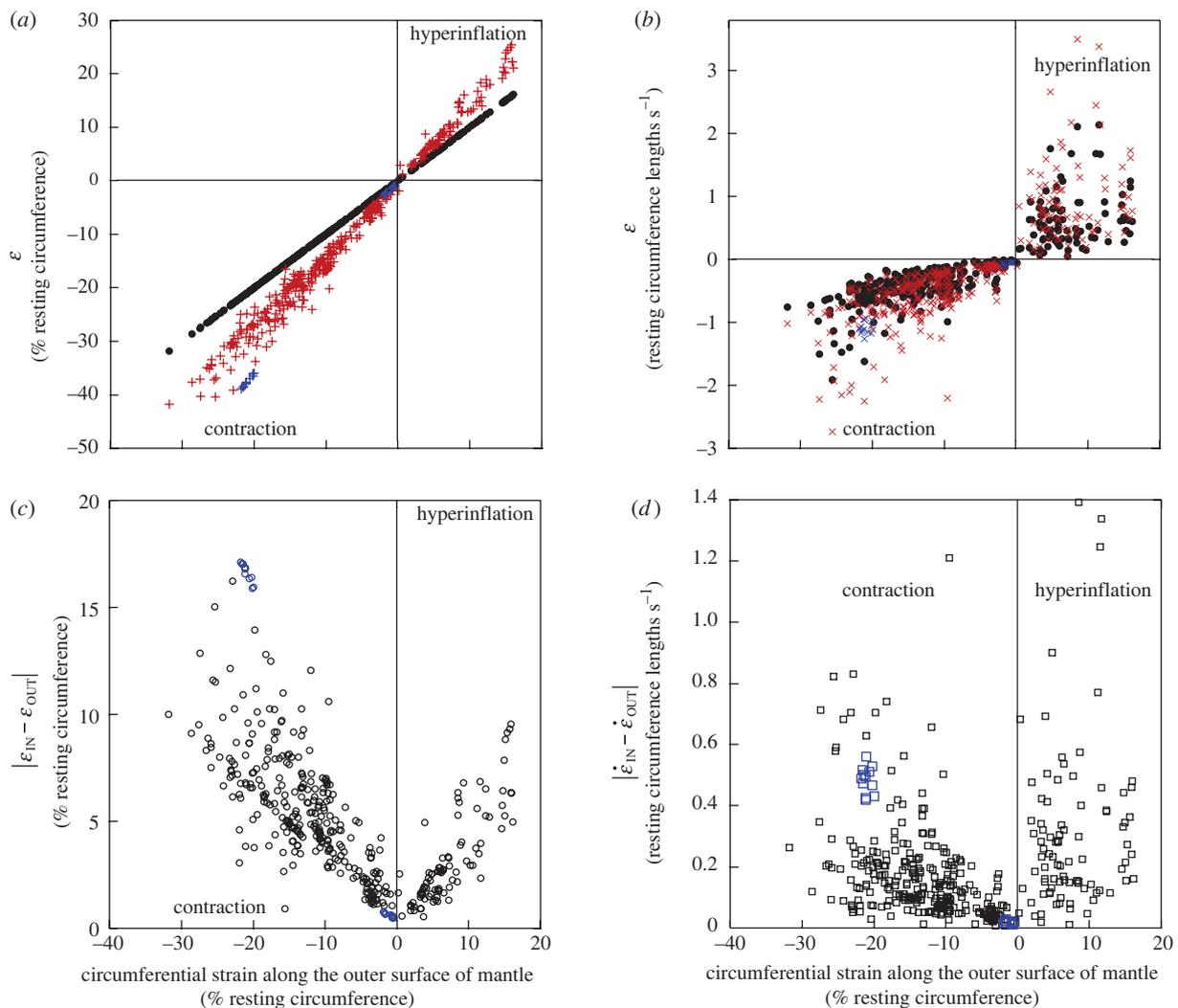


Figure 2. The circumferential strain,  $\epsilon$ , and strain rate,  $\dot{\epsilon}$ , of the inner and outer surfaces of the mantle as a function of the circumferential strain at the outer surface of the mantle for 288 jets from eight *D. pealeii* and 24 jets from two *S. lessoniana*. (a,b) show the total range of  $\epsilon$  and  $\dot{\epsilon}$  while (c,d) show the absolute value of differences in strain ( $|\epsilon_{IN} - \epsilon_{OUT}|$ ) and strain rate ( $|\dot{\epsilon}_{IN} - \dot{\epsilon}_{OUT}|$ ) between fibres at the inner and outer surfaces of the mantle. The strain rate data (b,d) exhibit greater scatter than the strain data (a,c) because for a given strain amplitude, an individual squid could alter strain rate considerably (i.e. a squid might produce a rapid, large amplitude mantle contraction followed by a relatively slow, large amplitude contraction). (a,b) Black filled circles, strain at outer surface, both species; red pluses, strain at inner surface, *D. pealeii*; blue pluses, strain at inner surface, *S. lessoniana*. (c) Black unfilled circles, difference in strain, *D. pealeii*; blue unfilled circles, difference in strain, *S. lessoniana*. (d) Black unfilled squares, difference in strain rate, *D. pealeii*; blue unfilled squares, difference in strain rate, *S. lessoniana*.

Soman *et al.* 2005). The body wall musculature of most soft-bodied invertebrates, including squid, is composed of obliquely striated fibres. The factors favouring the ubiquity of oblique striation are unknown, but experimental evidence from the obliquely striated fibres of leeches (Miller 1975) shows that such fibres can generate force over an impressive range of lengths. If the obliquely striated fibres of squids can similarly generate force over a wide range of lengths, then gradients of strain may have been a selective pressure favouring the evolution of oblique striation in the circular fibres.

It is often assumed that there are no regional differences in fibre strain within a striated muscle, though recent work on vertebrates has shown this assumption to be false (e.g. Huijing 1985; Pappas *et al.* 2002; Ahn *et al.* 2003; Higham *et al.* 2008). Our finding that fibres at different locations within the same muscular

organ experience very different strain and strain rates also contradicts this long-standing assumption. Furthermore, the mantle (indeed, the muscular organs and body walls of all soft-bodied invertebrates) is distinctive in that it lacks the aponeuroses or myotendinous junctions that are important contributors to non-uniform strain in vertebrate striated muscles.

It is interesting to note that studies of hollow cylindrical muscular organs in vertebrates, such as the mammalian heart and arteries, have not reported transmural gradients of muscle fibre strain. A gradient of strain is not observed in the left ventricle of mammals, for example, because relatively few muscle fibres within the thick myocardium simply wrap around the circumference of the ventricle. Rather, adjacent groups of fibres vary in their orientation as a function of position in the thickness of the ventricle wall (Anderson *et al.* 2009; Smerup *et al.* 2009). This

architecture virtually eliminates transmural gradients of strain and also permits the fibres to operate over a relatively small range of sarcomere lengths, while still ejecting most of the fluid from the ventricle chamber (e.g. MacGowan *et al.* 1997). By contrast, fibre orientation appears uniform among the striated circular muscles of invertebrate body walls (e.g. Trueman 1975), and gradients of strain and strain rate in circular muscle layers may therefore be universal among soft-bodied invertebrates.

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