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MECHANICS OF JET PROPULSION IN THE HYDROMEDUSAN JELLYFISH, *POLYORCHIS PENICILLATUS*

II. ENERGETICS OF THE JET CYCLE

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SUMMARY

The mechanical energy generated by the contraction of the subumbrellar swimming muscles to power the jet cycle in the hydromedusan jellyfish *Polyorchis penicillatus* (Eschscholtz, 1829) was measured. This energy was experimentally partitioned into three components during the contraction. The sum of these components was taken to be the mechanical energy generated by the muscles during the jet cycle and was between $8{\cdot}9\times10^{-5}$ and $1{\cdot}4\times10^{-4}$ J per contraction. Energy from one of these components is stored as strain energy in the mesoglea and powers the refilling phase. The mesoglea can clearly act as an effective elastic structure to antagonize the contraction of the swimming muscles completely, and it may be designed to function at some optimum. The mechanical significance of elastic energy storage systems in jet-propelled animals is discussed, and this significance is clearly displayed in *Polyorchis*. The unusually long-duration action potential of the swimming muscles may be an important component of the swimming mechanism, allowing the muscles to store energy in an elastic structure at the end of the contraction phase when little hydrodynamic thrust is developed. It is suggested that the action potential of vertebrate cardiac muscle may have a similar mechanical function.

INTRODUCTION

Animals swim by moving various parts of their bodies to do work on the environment, and the mechanical energy required to do this work is generated by contraction of muscles driving the locomotor apparatus. Unfortunately, it is often difficult to quantify the total mechanical cost of doing this work because some of the energy generated by the muscles does not contribute directly to the hydrodynamic work that generates the thrust, but is used for other purposes, and some is lost through dissipative processes as heat. The energy that does not generate thrust may be a substantial portion of the total mechanical energy generated by the muscles. Thus, any detailed study of the energetics of locomotion should not be based

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exclusively on an analysis of generation of thrust, but based on an analysis of the total mechanical energy generated by the muscles, including both the energy used directly to generate the thrust and the energies mentioned previously. These analyses are complicated in most animals, however, by musculoskeletal systems that generate complex temporal and spatial movements of the locomotor apparatus. These restrict our ability to make the mechanical and physiological measurements that are necessary for a detailed understanding of the energetics of locomotion.

These analyses are relatively simple in the hydromedusan jellyfish used in this study, since the locomotor system is comparatively simple. The locomotor apparatus has already been described in detail (Gladfelter, 1972; DeMont & Gosline, 1988*a*). Most of the bell consists of transparent, non-cellular mesoglea that is traversed by numerous radially arranged fibres. Circular muscles line the subumbrellar surface and power the locomotor cycle. The cycle is initiated by contraction of these swimming muscles, which reduces the diameter of the bell. Water contained in the bell cavity is ejected through the orifice surrounded by the velum, and the animal is propelled in the opposite direction. Recoil of the bell to resting dimensions is a passive process, powered by energy that is probably stored in the radial fibres during the deformation of the bell (DeMont & Gosline, 1988*a*). No muscles exist to power re-expansion.

This paper will describe efforts to measure the mechanical energies generated through the entire jet cycle of a hydromedusan jellyfish. The energy generated by the contraction of the subumbrellar swimming muscles performs three functions: (1) it generates the pressure in the subumbrellar cavity, (2) it overcomes the inertia of the movement of the bell, and (3) it deforms the tissue. The energy associated with the first component is used directly to generate the thrust that will propel the animal. The second and third components do not contribute directly to the generation of the thrust, but are nonetheless essential for the cycle to proceed. The inertial component makes both negative and positive contributions to the generation of the jet, since during the initial acceleration of the bell inwards, the inertia tends to act against the contraction of the swimming muscles, but when the muscles are relaxing near the end of the contraction phase, the inertia acts with the muscles. The elastic energy stored in the deformation of the mesogleal tissue will be used to power the refilling of the bell when the swimming muscles relax, and therefore all the energy required to power the jet cycle is generated by a single set of muscles during the contraction phase.

MATERIALS AND METHODS

The jellyfish used in this study, the hydromedusan *Polyorchis penicillatus*, were obtained from Bamfield Inlet, on the west coast of Vancouver Island. They were maintained in running seawater aquaria until used.

The purpose of the experimental portion of this study was to obtain accurate records of the pressure and volume changes occurring in the subumbrellar cavity during spontaneous contractions of the subumbrellar muscles. The procedures described below have been used in a similar analysis of the energetics of the jet cycle in squid (Gosline & Shadwick, 1983). Live *Polyorchis* were anaesthetized in isotonic magnesium chloride (Gladfelter, 1972), and the manubrium and gonads were removed. These animals were then tethered by gluing the apex of the bell (with cyanoacrylate adhesive) to a solid base. Pressure records were obtained by inserting a seawater-filled polyethylene catheter tube (PE 190) through the velum aperture and into the subumbrellar cavity. The end of the tube was placed as close to the base of the peduncle as possible, without coming into physical contact with it. The PE tube was attached at the other end to a Narco Telecare RP-1500i pressure transducer. The transducer was calibrated against known volumes of sea water, and the dynamic response was determined by monitoring free resonant vibrations from a pressure transient applied at the catheter tip (Gabe, 1972). The resonant frequency was 15 Hz, with a damping factor of 0·162 for the data analysed in this paper. The signal from the transducer was conditioned with a Gould (Model 13-4615-50) transducer amplifier and amplified with a Gould medium gain d.c. preamplifier (Model 13-4615-10). The signal was filtered with a 15 Hz filter installed in the preamplifier. To account for errors introduced by the filter, the characteristics of the filter were measured with a Wavetek Model 5820A cross channel spectrum analyser (Rockleigh, NJ). Procedures for the corrections are described below. The filtered signal was recorded on a Hewlett–Packard instrumentation tape recorder (Model 3964A).

Measurements of the subumbrellar cavity volume were obtained by monitoring the internal diameter of the bell with a video measuring system. This system uses a video dimension analyser (VDA) (Model 303, Instruments for Physiology and Medicine, San Diego, CA) that provides an electrical signal which is proportional to the separation of two contrast boundaries on any horizontal line in the video image. The bell of the jellyfish is transparent; thus it was possible to adjust the intensity of the incident light in such a way that the VDA triggered off the inside surface of the bell. Since the subumbrellar cavity is essentially cylindrical in shape, with a circular cross-section (Gladfelter, 1972), diameter measurements were easily converted into volume measurements. The signal of the VDA passes through a 15 Hz filter, which may also introduce errors in dynamic signals. To account for these errors, the characteristics of the filter were measured with the spectrum analyser, and corrections were applied as described below. The output of the VDA was recorded simultaneously with the pressure records as described above.

Selected segments of the analogue pressure and VDA records were digitized on a Digital Equipment Corporation MINC-11/23 computer for further analysis. The pressures measured in the subumbrellar cavity were very small, thus the signal-to-noise ratio was improved by digital signal averaging. A particularly clean sequence of pressure and VDA records from 13 contractions of the subumbrellar muscles was digitized at a rate of 200 points s^{-1} and signal-averaged. It was found that the final signal-averaged waveforms were slightly temporally asynchronous, in that the position in time where the pressure goes negative was shifted by about 50 ms from the time where the bell started to open at the beginning of the refilling phase. These events should occur simultaneously. Errors introduced by the filters in both the pressure amplifier and the VDA caused small temporal shifts in the two signals, and this resulted in the slight asynchrony in the two waveforms.

To correct for this problem, both the signal-averaged pressure and VDA records were passed through a Fourier analysis. The characteristics of the filters installed in the Gould pre-amplifier and the VDA were programmed appropriately to correct each of the harmonics in the power spectrum of both the pressure and VDA signals. In addition, the dynamic responses of the pressure transducer and the PE tubing attached to it were programmed to make an additional correction to each harmonic of the pressure waveform. This procedure is described in McDonald (1974). These corrected power spectrums were then resynthesized into their original time domains, and these corrected waveforms were used for further analysis, as explained in Results.

RESULTS

The contraction phase

All the energy required to power the jet cycle is generated by the contraction of the muscles during this phase. This energy can be quantified by measuring separately the energies associated with the three components listed in the Introduction. The energies of the pressure–volume work and the inertial work can be measured from records of the pressure and diameter changes of the subumbrellar cavity that occur during a contraction of the muscles. These measurements will be described next. The energies associated with the deformation of the bell were measured in the previous paper (DeMont & Gosline, 1988*a*) and will be described last.

Fig. 1 shows records of the original pressure and diameter changes that were used in this analysis. These data were processed as described above, and a signal-averaged, Fourier-corrected pressure–volume loop was generated (Fig. 2). The bell

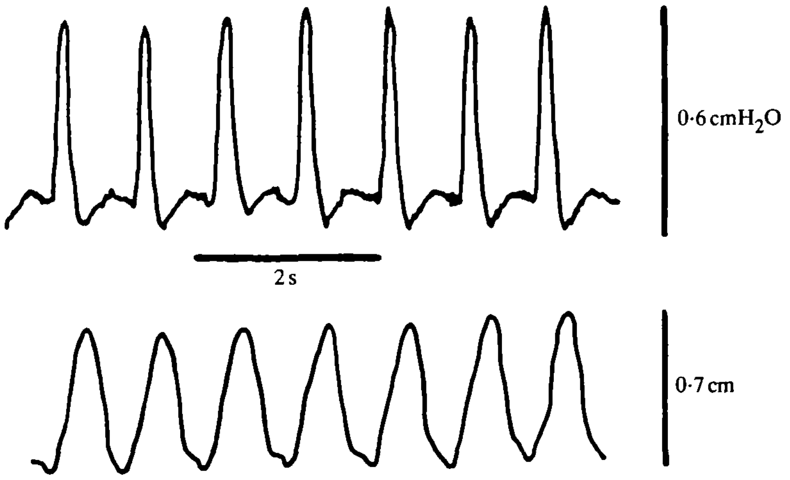

Fig. 1. Typical curves of pressure–diameter data used to generate the pressure–volume curve of Fig. 2. 1 cmH$_2$O = 98·1 Pa.

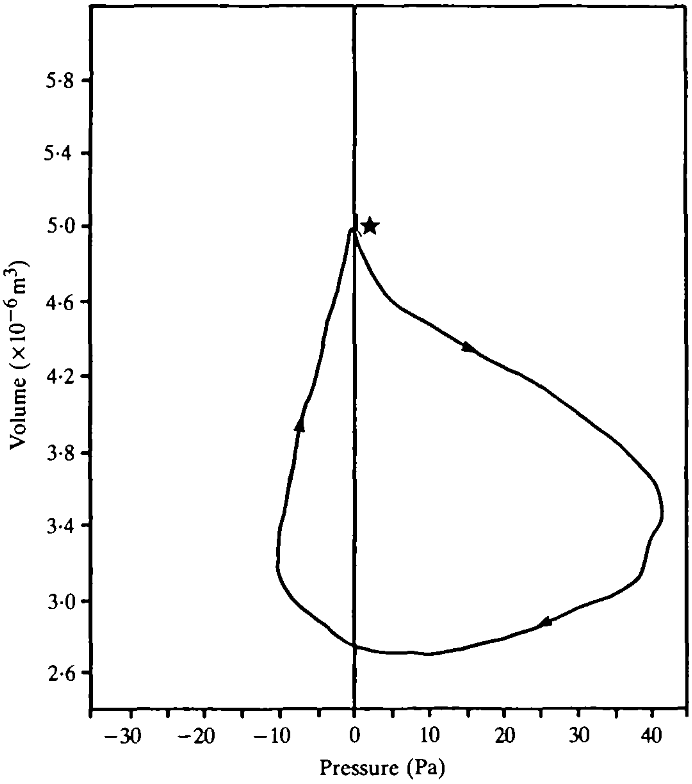

Fig. 2. A pressure–volume loop for the locomotor cycle of a hydromedusan jellyfish. The solid line is a signal-averaged, Fourier-corrected data set derived from a train of 13 pulses taken randomly from a long train of continuous contractions. The arrows indicate the direction of the contraction. The star indicates the start of the cycle.

height of the animal used in this portion of the study was 3·0 cm, and its mass was 7·3 g.

The pressure–volume record shows the events that occur in the middle of a long train of continuous contractions. The subumbrellar muscles start to contract near the point marked with a star, and the contraction phase of the cycle is initiated. As the contraction proceeds, the pressure in the cavity starts to rise and peaks at about 43 Pa. This occurs when about 65 % of the total volume of ejected water has been removed. The pressure then drops back to zero and the contraction phase of the cycle is complete. The area enclosed by the curve represents the total amount of energy that the muscles produce in generating the pressure in the subumbrellar cavity and is $5{\cdot}4\times10^{-5}$ J (see Table 1).

Inertial forces associated with the accelerations of the body wall cannot be measured directly from Fig. 2. Estimates of the acceleration of the body wall, which are necessary for the calculation of the inertial force, can however be derived from the original diameter measurements used to calculate the volume data shown in Fig. 2. To be consistent with other parameters used in the following calculations of the

Table 1. *Summary of components of energy generated by the muscles in the jet cycle of* Polyorchis penicillatus

Component of energy generated by muscles	Energy ($\times 10^{-5}$ J)	Percentage of total
Contraction phase		
(A) Pressure in subumbrellar cavity	5·4	61 % (min), 39 % (max)
(B) Inertia of wall	1·7 (min), 4·5 (max)	19 % (min), 32 % (max)
(C) Deformation of wall	1·8 (min), 4·1 (max)	20 % (min), 29 % (max)
Total	8·9 (min), 14·0 (max)	
Refilling phase		
(A) Pressure in subumbrellar cavity	1·3	76 % (min), 62 % (max)
(B) Inertia of wall	0·4 (min), 0·8 (max)	21 % (min), 39 % (max)
Total	1·7 (min), 2·1 (max)	

inertial force (e.g. the effective mass), diameter has been converted to circumference, and therefore displacement is expressed as a change in the circumference of the bell wall. The second derivative of circumference with respect to time is a direct measure of the acceleration of the body wall. This can be calculated by first measuring the instantaneous slope between two successive digitized points (5 ms apart), which is the first derivative of the circumference curve. The process is then repeated on the first derivative data, and this provides the second derivative, or the acceleration of the body wall. Small fluctuations in the initial diameter curve will be amplified using this method, and therefore a five-step running average was used to smooth out any small perturbations.

The mass of the body that is being accelerated also has to be known in calculating the inertial force, since the inertial force is equal to the product of the actual mass that is being accelerated and the acceleration. The mass of the accelerated body in this case includes the mass of the accelerated portion of the animal and the mass of both the water contained in the subumbrellar cavity and the water that surrounds the bell and is accelerated during the contraction of the bell. This effective mass cannot be measured directly, but it can be predicted using data from the following paper (DeMont & Gosline, 1988*b*), where the locomotor structure of the jellyfish is modelled as a harmonically forced damped oscillator. The model predicts that the effective mass should be between 2·5 and 6·2 times larger than the mass of the animal. Using these values, the effective mass in this study is predicted to be between 0·0183 and 0·0453 kg. The inertial force can be calculated at each time interval by multiplying the effective mass by the acceleration of the body wall.

The inertial forces calculated using this method are not the true inertial forces that the bell wall experiences during the jet cycle. This is because the real effective mass of the oscillating bell must fluctuate over the duration of the contraction, since the volume of fluid in the subumbrellar cavity changes during the jet cycle. The effective

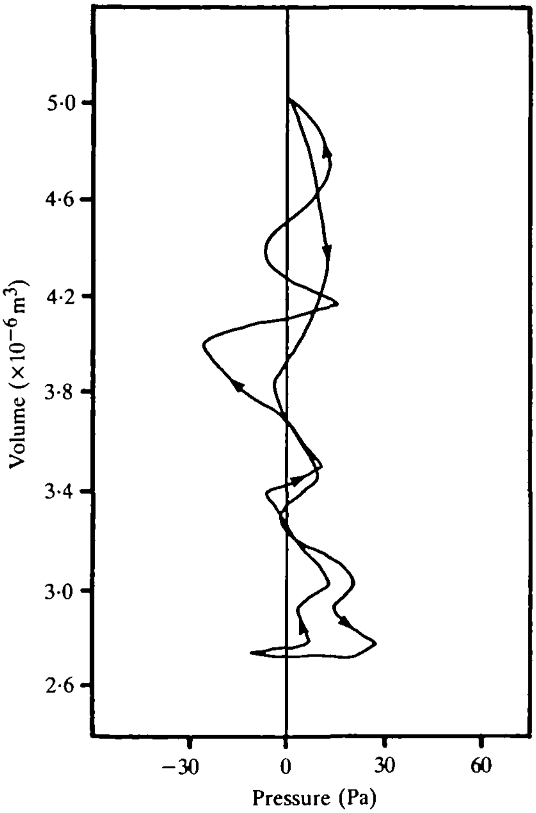

Fig. 3. Inertial pressures generated during the contraction of the locomotor muscles. The mass of the accelerated body was taken to be 0·0183 kg. The arrows indicate the direction of the contraction.

mass we have calculated is thus an average value, and we are unable to measure the temporal changes of the true inertial forces. The values calculated provide an averaged estimate of the inertial forces, and these will be used in comparisons with the total energies generated in the other components listed above.

The purpose of this analysis is to compare the components of the energies generated by the muscles. Thus the inertial force calculated as the product of the effective mass and the acceleration was converted to inertial 'pressure' by dividing the inertial force by the instantaneous surface area of the inside of the subumbrellar cavity, since this is the area that the calculated force was working on. Fig. 3 shows the calculated inertial pressures generated during the contraction cycle. The pressures change sign at various stages in the cycle. These indicate that the sign of the acceleration of the body wall is changing. The energies associated with the inertia of the wall can be measured directly from these curves as the area enclosed by the loops. The net energy used was taken as the sum of the positive and the negative contributions of the areas inside the curve. The net energy associated with the inertia of the wall during the contraction is $1{\cdot}7\times10^{-6}$ J with the lower range for the effective mass used in the calculation of the inertial force, and $4{\cdot}5\times10^{-6}$ J with the upper range of the effective mass used in the calculation. These calculations are the first records of the inertia of the body wall associated with its movement during the jet cycle of any jet-propelled animal.

A portion of the energy generated by the contraction of the muscles is used to deform the tissue. Data on the quantities of energy required to deform the tissue were collected as described in the preceding paper (DeMont & Gosline, 1988*a*). The quantity of energy is dependent on the rate at which the tissue is deformed, and it was difficult to measure the energy required to deform the tissue at the natural rate of contraction. The quantity of energy required, however, was estimated to be between $1{\cdot}8\times10^{-5}$ and $4{\cdot}1\times10^{-5}$ J.

The refilling phase

The contraction phase ends as the pressure in the subumbrellar cavity becomes negative and the bell starts to re-expand. The energy to power the refilling of the subumbrellar cavity comes exclusively from the potential energy stored as strain energy in the deformed bell. The total energy used can be measured with methods similar to those described above for the contraction. The energy used to generate the pressure in the subumbrellar cavity during refilling is equal to the area under the refilling phase of the loop in Fig. 2. Inertial pressures were calculated as before, and these data are shown in Fig. 3. The energy used in generating the pressure in the subumbrellar cavity is $1{\cdot}3\times10^{-5}$ J, while the net energy used in generating the inertial pressure is between $3{\cdot}5\times10^{-6}$ and $8{\cdot}2\times10^{-6}$ J. The total energy used in refilling the subumbrellar cavity can be approximated by simply adding the energies associated with the inertial pressure and the subumbrellar cavity pressure. This energy is between $1{\cdot}7\times10^{-5}$ and $2{\cdot}1\times10^{-5}$ J. These results are summarized in Table 1.

DISCUSSION

This paper reports the mechanical energy generated during the jet cycle of the hydromedusan jellyfish *Polyorchis penicillatus*. The cost of this locomotion cannot be quantified simply by measuring the cost of generating thrust. The calculation of all the mechanical energy generated by the contraction of the swimming muscles is relatively easy in the hydromedusan jellyfish studied here (Table 1). In the contraction phase of the jet cycle, the largest component of the total energy is associated with the pressure–volume changes in the subumbrellar cavity. This process requires $5{\cdot}4\times10^{-5}$ J of mechanical energy, and represents between 39 and 61 % of the total mechanical energy generated during the contraction. The energy associated with the inertia of the bell, between $1{\cdot}7\times10^{-5}$ and $4{\cdot}5\times10^{-5}$ J, is considerably smaller. It accounts for only between 19 and 32 % of the total energy generated. The amount of energy required to deform the locomotor structure is between $1{\cdot}8\times10^{-5}$ and $4{\cdot}1\times10^{-5}$ J, and this represents between 20 and 29 % of the total mechanical energy generated during the contraction. A simple summation of these three components gives an approximate value of the total mechanical energy that is used to generate the jet, and this summation yields a value between $8{\cdot}9\times10^{-5}$ and $1{\cdot}4\times10^{-4}$ J.

These values can now be compared to previous independent estimates of power requirements for jet propulsion in four other hydromedusae, *Gonionemus vertens* and *Stomotoca atra* (Daniel, 1985) and *Chelophyes* and *Abylopsis* (Bone & Trueman, 1982). Daniel measured the oxygen consumption of swimming medusae as a function of swimming frequency and was able to measure the power requirements of this process. He also predicted the power requirements with a model based on the balance of forces the animals must experience during locomotion, assuming a muscle efficiency of between 0·1 and 0·2. His predicted and measured values of the power requirements were in good agreement. The values for energy from Table 1 can be used to measure the equivalent power requirements. The entire cycle was completed in about 0·8 s, giving a power output of between $8{\cdot}8\times10^{-5}$ and $1{\cdot}4\times10^{-4}$ W. To correct for size differences, Daniel divided the power requirements by mass to the power of 5/3. For measured power requirements from Table 1, this gives a value of between 0·33 and 0·52 W $\mathrm{kg}^{-5/3}$. These values fall nicely in the cluster of data of his fig. 6, where the range of values is between about 0·2 and 0·75 W $\mathrm{kg}^{-5/3}$.

Bone & Trueman (1982) measured the total work per cycle as simply the pressure in the subumbrellar cavity times the volume of water ejected. They measured the pressure in the subumbrellar cavity using methods similar to those described for this work. Volume changes were measured by integration of the pressure pulse. They argued that this method is possible since jet efflux velocity during the exhalant phase depends upon the difference between chamber pressure and ambient pressure. Volume changes will necessarily follow pressure changes, and can be obtained indirectly by integration of the pressure pulse. Their estimated power outputs using this method were calculated to be between $3{\cdot}24\times10^{-5}$ and $1{\cdot}35\times10^{-4}$ W for *Abylopsis* and between $3{\cdot}88\times10^{-4}$ and $7{\cdot}76\times10^{-4}$ W for *Chelophyes*. These estimates agree reasonably well with estimates of the power output for *Polyorchis* ($8{\cdot}8\times10^{-5}$ to $1{\cdot}4\times10^{-4}$ W). Bone & Trueman did not, however, provide the masses of the animals used in their study, so comparisons similar to those made with Daniel's work cannot be made.

How do the stresses generated by the swimming muscles during the cycle compare with stresses generated by other muscles? The maximum stress generated by the swimming muscles can be approximated by using the equation for the circumferential stress in a thin-walled cylinder, $\sigma = PR/t$, where P is pressure, R is radius and t is wall thickness. This calculation will necessarily be an underestimate of the real stress generated by the swimming muscles, since this calculation assumes that the swimming muscles only do work to generate the pressure in the cavity, and it has already been shown that this is not true. The maximum pressure generated during the contraction is about 40 Pa (see Fig. 2), and this is reached at a radius of about $6{\cdot}3\times10^{-3}$ m. The thickness of the subumbrellar layer of swimming muscles was taken from Gladfelter (1972) to be 2×10^{-6} m. Substitution of these values into the equation for the circumferential stress in a thin-walled cylinder yields a maximum stress for the muscles of about $1{\cdot}25\times10^5\,\mathrm{N\,m^{-2}}$. Using similar methods, Bone & Trueman (1982) predicted a maximum stress of about $2\times10^5\,\mathrm{N\,m^{-2}}$ for *Chelophyes*. For comparison, the maximum isometric stress of almost all striated muscles falls in the range 3×10^5 to $5\times10^5\,\mathrm{N\,m^{-2}}$ (Alexander & Goldspink, 1977).

A substantial proportion of the total mechanical energy generated in this process is used to deform the tissue during the contraction. This energy might at first appear to have been used at the expense of generating mechanical energy that could have done useful hydrodynamic work. This is not true, however, and the reasons will be clear when the mechanics of such an elastic storage system are explained below.

The mechanical significance of elastic strain energy storage systems in jet-propelled animals is noteworthy, and has already been described in some detail for jet-propelled swimming in squid (Gosline & Shadwick, 1983; Gosline & DeMont, 1985). The elastic energy storage system in squid mantle plays a very important role in its swimming mechanics, and the locomotor system of the jellyfish is mechanically similar to that found in the squid. First, the squid is geometrically similar, in that fluid contained in a thick-walled cylindrical chamber is expelled through an orifice at one end, generating a jet that propels the animal in the opposite direction. The ejection of the water is caused by the contraction of circular muscles in the wall of the chamber, which decreases the diameter of the wall, and there is a concomitant increase in the wall thickness. This occurs because the squid mantle, like the bell of the jellyfish, is a constant volume system, and there is a negligible change in the length of the cylinder during the contraction. Second, during the contraction of the circular muscles in the squid mantle, elastic fibres embedded in the mantle wall are put in tension as the wall thickness increases, and strain energy is stored.

The elastic structures in squid mantle store the strain energy at a time in the jet cycle when the full mechanical output of the muscles cannot be used to generate hydrodynamic thrust (Gosline & Shadwick, 1983). This is true on geometrical arguments alone, since by virtue of the cylindrical shape of the locomotor system, the volume of fluid expelled during the contraction phase of the jet cycle is proportional to the change in the radius squared, and the ability of the muscle to impart energy to the confined fluid is directly proportional to the change in radius. Therefore, the potential for doing hydrodynamic work in a cylindrical system must decrease as the contraction proceeds, even though the potential for muscles to do work remains unchanged. Thus, since squid probably keep the muscles active during the entire contraction phase, they are able to increase the total output of their muscles by storing the extra output in the elastic structures of the mantle.

It has been proposed that a nonlinear stress–strain curve for the elastic structure in squid mantle would be the most functional of designs, as the initial low modulus region would allow the mantle to deform easily when the potential hydrodynamic output is high, but near the end of the contraction the increasing stiffness of the elastic structure would allow the storage of strain energy when the potential for hydrodynamic work is low. This potential energy stored in the elastic structure would then be used later in the cycle to power the re-expansion of the mantle, without significant loss of hydrodynamic thrust.

In squid, during slow respiratory jet movements, the refilling phase is powered completely by energy released from the storage system (Gosline, Steeves, Harman & DeMont, 1983), and thus energy generated by the contraction of the circular muscles powers the entire jet cycle. The cost of this locomotion is important, since this mode is used for normal steady swimming. Unlike the jellyfish studied in this work, squid have radial muscles which can partially, or completely, power the refilling phase of the jet cycle. These radial muscles are probably active only during rapid escape jets, when the absolute cost of locomotion is not of primary importance. The escape jet is used to avoid predation, and increasing the rate of the cycle for maximum acceleration would be most beneficial.

The jellyfish studied in this work maintain themselves in the water column by contracting in continuous bouts of about 10–20 bell contractions. These bouts of contraction are analogous to the slow respiratory jet movements seen in squid. As for the squid, the costs of this locomotion are important, and the jellyfish would benefit by taking advantage of the mechanisms described above. In fact, the significance of elastic strain energy storage systems is remarkably displayed in the jellyfish studied in this paper. First, a nonlinear stress–strain curve was found for the locomotor structure (DeMont & Gosline, 1988*a*), and thus these animals are clearly taking advantage of the mechanisms described above. That is, the design of the energy storage system allows the same muscle to power both the contraction phase and the refilling phase of the cycle. Second, and quite remarkably, these animals appear to have adopted another important physiological character to take advantage of the nonlinearity of the energy storage system. Spencer & Satterlie (1981) found an unusual action potential in the swimming muscle of *Polyorchis*. The action potential has a square waveform, which probably maintains the excitation–contraction processes of the swimming muscles in the active state for long periods. They suggest that the functional significance of this unusually long action potential is that most of the water in the subumbrellar cavity can be ejected, and this is important in generating large propulsive forces. We suggest that this unusual action potential probably functions not so much to generate larger hydrodynamic forces, as the potential for generating such forces necessarily decreases as the contraction continues. Rather, it allows sufficient deformation of the elastic structure late in the contraction phase to store enough strain energy to antagonize the swimming muscles during the recovery phase when the bell expands.

Spencer & Satterlie (1981) also suggested that the distinct plateau in cardiac muscle action potential may have a similar functional significance, to maximize fluid expulsion from the heart. We suggest, however, that the extended action potential in cardiac muscle may allow the muscles of the heart to deform elastic structures and store strain energy during periods when functionally significant hydrodynamic work cannot be done. This stored strain energy would then be available to help restore the contracted heart to its resting state and aid in the refilling of the heart. But this would be true only if vertebrate hearts functioned mechanically as suction pumps, like squid and jellyfish. In the light of a recent new model proposed for the functioning of the vertebrate heart, where it is suggested that hearts do indeed function as mechanical suction pumps (Robinson, Factor & Sonnenblick, 1986), then the square waveform action potential of cardiac muscle may well have the mechanical function described above.

In the previous paper (DeMont & Gosline, 1988*a*), it was shown that the isolated mesoglea comprising the system has a dynamic resilience of about 58 %. This implies that after the release of the stored strain energy, with its associated viscous losses, the original energy will be reduced to between $1{\cdot}1\times10^{-5}$ and $2{\cdot}4\times10^{-5}$ J of energy left to power the refilling phase. The energy required to power the refilling phase was shown to be between $1{\cdot}7\times10^{-5}$ and $2{\cdot}1\times10^{-5}$ J. These results verify that the mesoglea can act as an effective elastic structure that can completely power the refilling phase.

It is tempting to suggest, in the light of the remarkable similarity in magnitude between the energy available and energy required for the refilling phase, that the storage system is tuned to function at some optimum level. This idea is explored in considerable detail in DeMont & Gosline (1988*b*). The 'tuning', in summary, is related to a physical phenomenon called resonance, and we show that the swimming muscles force the locomotor structure to oscillate at its resonant frequency and consequently reduce the mechanical cost of jet propulsion.

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