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ONE

Functions of Elastomeric Proteins in Animals

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INTRODUCTION

Elastomeric proteins play many important roles in the lives of animals. They enable animals ranging from fleas to large mammals to jump further than would otherwise be possible. They save energy in locomotion for galloping horses, hopping kangaroos, flying flies, and swimming jellyfish. They make clam shells spring open when the muscles inside relax, they help to support the heavy heads of cattle, they smooth the flow of blood round our bodies, and they cushion the impact of our heels on the ground. This chapter attempts to explain briefly how they do all these things.

POWER AMPLIFIERS

Catapults are power amplifiers. The rubber is stretched in preparation for shooting, storing up strain energy. This can be done slowly; but when the catapult is released, the rubber recoils very rapidly, returning the stored energy as kinetic energy of the missile. The work done by the recoiling rubber is (almost) equal to the work previously done stretching the rubber; but, it is done in a much shorter time so the power (rate of doing work) has been amplified. Using a catapult, I can project a missile much faster than I can move my hand.

Catapults are useful because the power output that can be obtained from a muscle is limited. For example, Peplowski and Marsh (1997) made physiological measurements on a leg muscle of a tree frog and found that the highest power output obtainable from it was 240 W/kg. However, they calculated that the power required for the longest jumps, which it could make at the same temperature, was about 800 W/kg muscle. They concluded that a catapult mechanism must be involved.

The best-known examples of catapult mechanisms in animals are in jumping insects. The importance of the catapult principle was first demonstrated by Bennet-Clark and Lucey (1967) in a study of the flea *Spilopsyllus*. This insect is about 1.5 mm long. It jumps by rapidly extending its hind legs, accelerating itself

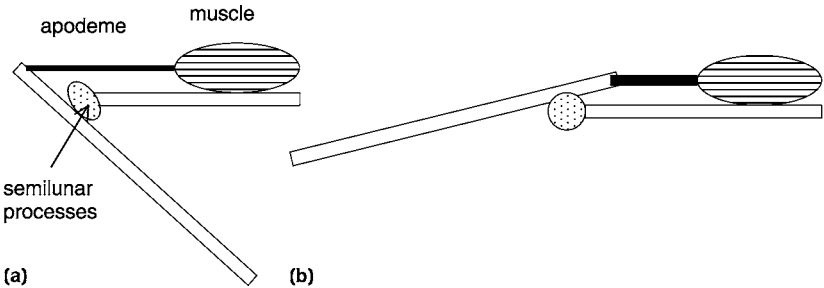


Figure 1.1: Diagrams of a locust knee (a) bent with the muscle taut and (b) extended. The extensor apodeme is stretched and the semilunar process is compressed in (a).

from rest to its take-off velocity of 1 m/s in a distance of 0.4 mm. This implies (assuming constant acceleration) that the legs extend in 0.8 m/s. No known muscle can complete an isolated contraction in as short a time as this (though the fibrillar flight muscles of some small insects are capable of oscillating the wings at 1000 Hz). Bennet-Clark and Lucey (1967) showed that the flea's springs are blocks of the rubbery protein resilin at the bases of the hind legs. They confirmed that these blocks were amply large enough to store the energy of the jump and demonstrated a locking mechanism that prevents the resilin from recoiling until the flea is ready to jump.

Subsequent research led to the discovery of catapult mechanisms in other insects, including locusts, click beetles, and flea beetles (see Gronenberg, 1996). The springs can be arranged in either or both of two principal ways. Both arrangements are found in locusts (Bennet-Clark, 1975) and are illustrated in Figure 1.1. The jump is powered by the extensor muscle of the 'knee' joint. One of the springs is the apodeme, through which the muscle attaches to the skeleton. The other is a structure in the joint known as the semilunar process. Both consist of chitin fibres in a protein matrix. Initially, the joint is locked by a catch, in the bent position [Figure 1.1(a)]. Contraction of the muscle stretches the apodeme and compresses the joint, storing up strain energy in both. When the catch is released, both springs recoil, allowing the animal to jump.

Springs can amplify the power available for jumping, even (as seems to be the case in frogs) when there is no mechanism to lock the joints. This point is illustrated by a simple mathematical model of jumping that is designed to be applicable to the whole range of jumping animals, from fleas to humans (Alexander, 1995). Knee extensor muscles with elastic tendons power this model's jumps. The forces that the muscles can exert fall as the rate of shortening rises, according to Hill's equation (see textbooks on muscle physiology). Figure 1.2 shows examples of computer simulations of three styles of jumping. In Figure 1.2(a),

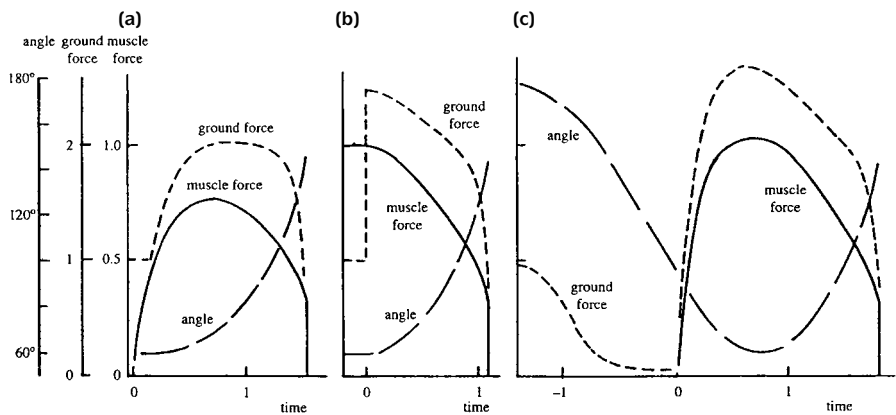


Figure 1.2: Computer simulations of standing jumps: (a) squat jump, (b) catapult jump, and (c) countermovement jump. The force exerted on the ground is expressed as a multiple of body weight, and the force exerted by the muscle that extends the leg is expressed as a multiple of its isometric force. Both these forces, and the angle of the knee joint, are plotted against a dimensionless time parameter. From Alexander (1995).

a squat jump, no catch is used. The animal starts with its knees bent. At time zero, it activates the knee extensor muscles. Initially, the muscles shorten quite rapidly, stretching their tendons as they develop force. As the tendons stretch, the force exerted by the muscles rises and their rate of shortening falls accordingly. However, because the muscles are still shortening, the force can never reach the isometric level that can be exerted only when the rate of shortening is zero. As knee extension continues at an ever-increasing rate, the rate of shortening of the muscles has to increase again, the force they exert falls, and the tendon starts to recoil. Eventually, the muscles are no longer able to exert enough force to maintain the angular acceleration of the legs and keep the feet on the ground. The model calculates the speed at which the animal leaves the ground and hence the height of the jump.

Figure 1.2(b) shows a catapult jump. In this case, there is a catch that is initially set. It keeps the knee bent while the muscle develops tension. At time zero, with the muscle exerting its isometric force, the catch is released and the force exerted by the feet on the ground rises abruptly to a high value. The force on the muscle falls as the tendon recoils elastically, and the lower force allows the muscle as well as the tendon to shorten. Eventually, the feet leave the ground.

Figure 1.2(c) shows a countermovement jump. As in Figure 1.2(a), there is no catch. The action does not start with the knee bent, as in the other cases, but with it straight. The jumper allows his or her body to fall, but activates the knee muscles before the knees are fully bent. The time of activation is adjusted so that the angle of the knees, at the bottom of the fall, is the same as the initial

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knee angle in Figure 1.2(a,b). During the fall, the muscle force may rise above the isometric level because the muscle is being stretched.

Alexander (1995) performed simulations for animals of different sizes. I gave each animal muscle properties that I judged to be typical, for jumping mammals or insects of its size. If the tendons had no elastic compliance, all three techniques gave jumps of the same height. When the tendons were given elastic compliance, all three techniques gave higher jumps, and the height of the jump depended on the technique. A human-sized model jumped about equally high in a catapult jump and a countermovement jump, and less high in a squat jump. An insect-sized model jumped much higher by the catapult technique than by either of the other techniques. Humans have no catch mechanism, so they cannot perform catapult jumps. They can jump a few centimetres higher in a countermovement jump than in a squat jump. Jumping insects, as we have seen, rely on catapult mechanisms.

Power-amplifying functions have also been postulated for a few structures that are not involved in jumping. Aerts et al. (1987) argued that there must be an elastic mechanism that amplifies power in suction feeding by fish. Gronenberg (1996) has described spring-loaded jaws in ants.

ENERGY STORES FOR RUNNING

A bouncing ball loses kinetic energy when it hits the ground, then immediately regains it by elastic recoil. A perfect ball in a frictionless world would continue bouncing forever.

This principle is important in running for large mammals such as ourselves. At each footfall, a runner loses and regains kinetic energy and gravitational potential energy. Cavagna et al. (1964) measured these energy fluctuations for men running at different speeds. They compared the energy fluctuations with the metabolic energy cost of running, calculated from measurements of oxygen consumption. These comparisons seemed to show that the muscles were working with much higher efficiencies than had been measured for other activities, such as walking up and down slopes, or pedalling a bicycle ergometer. Cavagna and colleagues argued that some of the kinetic plus gravitational potential energy lost and regained in each footfall must be stored briefly as elastic strain energy in the muscles, and returned in an elastic recoil. Energy must be saved by the principle of the bouncing ball.

A paper by Cavagna et al. (1964) gave the impression that the elastic compliance was in the muscles themselves. However, Alexander (1974) filmed a dog and recorded the forces that its feet exerted on the ground as it took off for a jump. The joint angle changes shown in the film implied that the gastrocnemius and plantaris muscle-tendon complexes stretched and then shortened by more than 20 mm while their feet were on the ground. I calculated that the peak

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forces on the tendons were enough to stretch them by this amount. This suggested that tendons might be the important energy-saving springs in the legs. A similar study of hopping by kangaroos (Alexander and Vernon, 1975) led to the conclusion that the gastrocnemius and plantaris tendons were indeed very important energy-saving springs.

Recent technical advances have made it possible to investigate the role of tendon elasticity more directly and more precisely. Biewener et al. (1998) performed surgical operations on wallabies, fitting tendon buckles to measure the forces in tendons and implanting sonomicrometry crystals to record the length changes of muscle fascicles. They showed that the fascicles of the gastrocnemius and plantaris muscles remained almost constant in length, while their tendons stretched and recoiled during the part of the hopping stride in which the foot was on the ground. They calculated that at 6 m/s (the fastest speed investigated), 45% of the energy that would otherwise have been needed for hopping was saved by elastic storage in tendons. Roberts et al. (1997) had performed a similar experiment on turkeys, with similar results.

The importance of tendon elasticity in running has also been demonstrated in other moderate-to-large mammals [e.g., in camels and horses (Alexander et al., 1982; Dimery et al., 1986; Biewener, 1998)] and in ostriches (Alexander et al., 1979). Muscles whose tendons are important as springs tend to have very short muscle fascicles. If tendon stretching allows most of the movement required at a joint, short muscle fascicles are sufficient to provide the rest of the movement. The shorter the fascicles, the less metabolic energy is required to maintain tension in them. In the extreme cases of the camel and horse, the fascicles of some of the distal leg muscles have almost disappeared, leaving tendons that run virtually uninterrupted from one skeletal attachment to the other, and must function as passive springs. Ker et al. (1987) showed that, in human running, the ligaments of the arch of the foot are important energy-saving springs, as well as the Achilles tendon.

Although tendon elasticity seems to give substantial energy saving in running for most large mammals, it appears to have very little importance in kangaroo rats (mass about 100 g; Biewener and Blickhan, 1988). These small mammals hop like kangaroos, but the tendons in their legs stretch very little. The reason seems to be that the forces that act when these animals jump are much larger than the forces of hopping. The tendons have to be thick enough to withstand jumping forces, so the stresses that act in them in hopping are small.

Alexander et al. (1985) identified another energy-saving spring in mammals that gallop. In the 'gathered' stage of a galloping stride, all four legs have to reverse their directions of swing. The forelegs have been moving backwards and must be made to swing forward; and the hind legs have been moving forward and must be made to swing back. We showed that much of the kinetic energy, which

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is lost and regained as the legs reverse, could be stored in the aponeurosis of the longissimus muscle. (An aponeurosis is a sheet of tendon, and the longissimus is the principal extensor muscle of the back.) Some more of the energy would be stored in the vertebral column, which would function as a compression spring. The elastic compliance of the vertebral column in compression is located partly in the intervertebral discs and partly in the bony centra.

ENERGY STORES IN FLIGHT AND SWIMMING

Energy can be saved by springs in other oscillatory movements. Weis-Fogh (1960) discovered the rubber-like protein resilin in the thoraxes of some insects and suggested that it might serve as an energy-saving spring. Insects fly by beating their wings, often at very high frequencies. In each wing beat cycle, the wings and the added masses of air that move with them are accelerated in one direction, halted, accelerated in the opposite direction, and halted again. The work required to give them this kinetic energy is called inertial work to distinguish it from the aerodynamic work that is needed to keep the animal airborne.

The need for the muscles to do inertial work can, in principle, be eliminated by springs that give the system a resonant frequency matching the wing beat frequency. Such springs would take the kinetic energy from the wings at the end of one stroke and return it by elastic recoil for the next. This would save energy if the inertial work was large compared with the aerodynamic work. However, if the inertial work is small, the kinetic energy taken from the wings can be used to do aerodynamic work, and there may be no advantage in having springs in the system. Wilmott and Ellington (1997) estimated for a hovering moth (*Manduca*) that the aerodynamic power requirement was 18–26 W/kg, and the inertial requirement 23–38 W/kg. In this case, there is potential for substantial energy savings by an elastic mechanism.

Weis-Fogh (1973) calculated the aerodynamic and inertial work required for hovering by various insects and compared it with the metabolic rates obtained from measurements of oxygen consumption. He calculated the efficiencies with which the work must be done if there was no elastic storage and if there was perfect elastic storage that entirely eliminated the need for the muscles to do inertial work. He concluded that some species must have energy-saving elastic mechanisms, because otherwise the muscles would have to work with impossibly high efficiencies. However, the metabolic rates that he used seemed in some cases to have been much too low, because the measurements were made on tethered insects whose wing beats may not have been strong enough to generate the aerodynamic forces needed for flight.

More recent calculations of the efficiency of insect flight have not given unambiguous evidence for elastic mechanisms. Possibly the best evidence for energy saving by elastic mechanisms in insect flight comes from an ingenious experiment by Dickinson and Lighton (1995), who stimulated a tethered fruit fly to

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attempt to turn alternately to either side, by means of a moving pattern of lights. In trying to turn, it varied the frequency and amplitude of its wing beats, making the ratio of inertial to aerodynamic power vary. Dickinson and Lighton measured the fly's oxygen consumption and correlated the fluctuations of oxygen consumption with the fluctuations of wing beat frequency and amplitude. Their analysis led to the conclusion that the muscles worked with an efficiency of 0.11 and that modest energy savings were made by elastic storage.

In principle, elastic mechanisms could be important in the flight of birds, as well as insects. Wells (1993) calculated that the wing muscles of hovering hummingbirds must work with an improbably high (but not necessarily impossible) efficiency of 25%, unless energy was saved by elastic storage. However, no elastic mechanisms that could save energy in bird flight have been convincingly demonstrated. Pennycuick and Lock (1976) suggested that wing feathers might be important springs, but Alexander (1988) gave reasons for thinking this implausible. Jenkins et al. (1988) took cine X-ray pictures of flying starlings and showed that the furcula bends and recoils in each wing beat cycle. It might be supposed that it was a potentially useful elastic energy store, but it can be shown from their data that the elastic strain energy it stores is very much less than the kinetic energy of the flapping wings, so it cannot be important.

Elastic energy-saving mechanisms may be important in swimming for some animals. For example, dolphins swim by beating their tail flukes up and down. The fluke, and the added mass of water that moves with it, loses and regains kinetic energy twice in each tail beat cycle. The tail muscles insert through numerous long, slender tendons. Bennett et al. (1987) measured the elastic compliances of these tendons and the vertebral column, and discussed the possibility that they might have an energy-saving role. Our data (reinterpreted by Blickhan and Cheng, 1994, in light of an improved hydrodynamic analysis) indicate that the compliance of the tendons has approximately the value required to eliminate the need for muscles to do negative work. This implies that they are rather more compliant than would be optimal, according to the theory of Alexander (1997), which is outlined in the following section.

Scallops (*Pecten*, etc.) are exceptional among bivalve molluscs in being able to swim. They do this by rapidly and repeatedly opening and closing their shells, ejecting jets of water on either side of the hinge. The shell is closed by means of a muscle, but there is no muscle to open it; instead, there is an elastic hinge ligament just inside the hinge. This is a block of the rubber-like protein abductin. It is compressed when the shell closes and recoils elastically to open it. The resonant frequency of the animal, due to the interaction of the compliance of the hinge ligament with the masses of the valves of the shell and the added masses of water that move with them, matches the frequency of the swimming movements. It has been suggested that the hinge ligament functions as an energy-saving spring, like the others described in this section. However, Cheng et al. (1996)

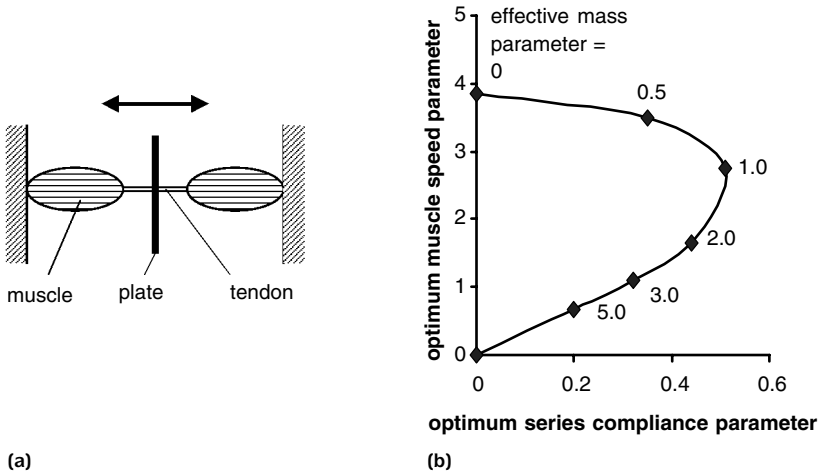


Figure 1.3: (a) Model of oscillatory motion powered by muscles. (b) Graph showing the combinations of muscle speed parameter and series compliance parameter that are predicted to minimise the metabolic power needed to drive the system for different effective mass parameters. Parameters are defined in the text.

showed that the inertial work of opening and closing the shell is tiny, compared with the hydrodynamic work required to power the jet; so, any energy-saving effect of the abductin is trivial.

Jellyfish also swim by jet propulsion, by repeatedly contracting and expanding their bells. Muscles contract the bell, but it expands by elastic recoil of the mesogloea. De Mont and Gosline (1988) showed that *Polyorchis* swims at its resonant frequency and that the inertial work requirements are large enough, compared with the hydrodynamic work, for the mesogloea to function as an energy-saving spring.

Alexander (1997) pointed out that all the activities that have been discussed in this section can be represented by the model shown in Figure 1.3(a). A pair of antagonistic muscles oscillate a plate in a fluid, doing inertial and hydrodynamic work as required. There are compliant tendons in series with the muscles, and there may also be a spring acting in parallel with the muscles. (The hinge ligament of scallops is an example of a parallel spring.) If the length changes of the muscles are calculated (taking account of tendon compliance), and also the forces that the muscles have to exert at each stage of a cycle, the metabolic rates of the muscles can be estimated. Unfortunately, my calculations of metabolic rate had to be based on physiological measurements on muscles making single contractions, because no suitable data on repetitive contractions were available. For this reason, rates calculated from the model may be to some extent misleading.

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To use the model, it is necessary to assign values to three parameters:

- Effective mass parameter – If there is no parallel spring, this is the ratio of the peak inertial force to the peak hydrodynamic force. A parallel spring reduces the effective mass parameter by exerting some of the required inertial force. If this spring has the compliance required to match the resonant frequency of the system to the frequency of the motion, the effective mass parameter is zero.
- Series compliance parameter – This is the amount by which the peak hydrodynamic force would stretch the tendons, divided by the amplitude of the motion.
- Muscle speed parameter – This is the maximum speed at which the muscles are capable of shortening (generally referred to by physiologists as v_{\max}), divided by the peak speed of the plate.

Calculations show that, for any given value of the effective mass parameter, there is an optimum combination of the other two parameters that minimise metabolic rate [Figure 1.3(b)]. When the effective mass parameter is zero, the optimum is a series compliance parameter of zero and a muscle speed parameter of 3.9; the muscles should not have compliant tendons and should be rather fast. As the effective mass parameter increases to about 1.2, the optimum compliance parameter rises to 0.5, and the optimum muscle speed parameter falls a little. As the effective mass parameter rises further, the optimum values for both the other parameters fall, approaching zero as the effective mass parameter approaches infinity.

Alexander (1997) compared the properties of muscles that drive oscillatory movements to the properties that the model predicted as optimal, in the few cases in which the data were available. Scallops swim at their resonant frequencies, so have an effective mass parameter of zero. The adductor muscle has no tendon, so the compliance parameter is zero; and measurements of its force/velocity properties gave muscle speed parameters of about four. Thus, this muscle seems to be very close to the predictions of the model. However, the effective mass parameter for a swimming dolphin is about 0.3, giving a predicted optimum compliance parameter of 0.22, whereas the actual value seems to be 0.67. (This discrepancy does not make much difference to the predicted energy cost of swimming, because the optimum is rather flat.) Because I know of no force/velocity experiments on dolphin muscle, I cannot calculate a muscle speed parameter. I do not have the data that would be needed to calculate either parameter for flying bumblebees (*Bombus*) or for hovering hummingbirds (*Amazilia*). The effective mass parameters for these two examples (assuming they do not have parallel springs) are about three and five, respectively.

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The model illustrated in Figure 1.3 can be applied to running, as well as to swimming. As an animal runs, its legs oscillate backwards and forwards. Also, the deceleration and reacceleration of the body that occur in each step can be regarded as an isolated half-cycle of an oscillation. The aerodynamic forces are trivial, so the effective mass parameter is extremely high. The optimum design predicted by the model would incorporate very slow muscles, with tendons of the right compliance to do all the inertial work. As noted in the previous section, mammals such as kangaroos, horses, and humans have distal leg muscles with long tendons and very short muscle fascicles (implying a low maximum shortening speed). However, the model ignores the need for fast muscles for acceleration and jumping. Mammals have fast muscles with long fascicles principally in the proximal parts of their legs.

RETURN SPRINGS

Bivalve molluscs have adductor muscles to close their shells, but no muscles to open them. Instead, the shell springs open by elastic recoil of the hinge ligament. We have already seen how the hinge ligament of scallops gives these molluscs a resonant frequency matching the frequency of their swimming movements. In other bivalves, which do not swim, the hinge ligament functions simply as a return spring that enables the animal to open the closed shell. The hinge ligament of scallops has low hysteresis, suiting its function in swimming, but the hinge ligaments of other bivalves show much more marked hysteresis (Trueman, 1953).

There are many other examples of elastic materials that serve as return springs in animals. Sea anemones, such as *Metridium*, can contract the body to a small conical mass or expand it to form a remarkably large, thin-walled cylinder. They contract by means of muscles and expand by using cilia to inflate themselves with water. The jellylike mesogloea in the body wall has viscoelastic properties (Alexander, 1962). If the muscles and cilia are put out of action by anaesthesia, the animal slowly becomes a small cylinder, whatever its initial size and shape. This implies that, when it is unstrained, the mesogloea is a small cylinder. The high hysteresis of the mesogloea seems appropriate for an animal that lives on shores attached to rocks. It is exposed to waves, with periods of the order of 10 s. The mesogloea resists waves reasonably well, but is easily stretched over periods of the order of an hour by the small pressures generated by the ciliary pump (see also Koehl, 1977).

Cicadas sing by oscillating the tymbal, a sheet of thin cuticle reinforced by a series of sclerotised ribs. A muscle pulls the tymbal inward to generate each group of sound pulses, but the tymbal springs out again elastically. In this case, the behaviour of the elastic structures is much more complex and interesting than that of a simple return spring. As the muscle contracts, the tymbal ribs