CHAPTER 3

Metrics of Natural Muscle Function

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3.1   Caution about Copying and Comparisons

Natural muscle is a spectacular actuator. Why? After millions of years, nature has evolved actuators that allow breathtaking performances. Cheetahs can run, dolphins can swim, and flies can fly like no artificial technology can. It is often argued that if human technology could mimic muscle, then biologicallike performance would follow. Unfortunately, the blind *copying* or mimicking of a part of nature [Ritzmann et al., 2000] does not often lead to the best design, for a host of reasons [Vogel, 1998]. Evolution works on the "just good enough" principle. Optimal designs are not the necessary end product of evolution. Multiple satisfactory solutions can result in similar performances. Animals do bring to our attention amazing designs, but these designs carry with them the baggage of their history. Why should these historical vestiges be incorporated into an artificial technology? Moreover, muscle design is constrained by factors that may have no relationship to human-engineered designs. Muscles must be able to grow over time, but still function along the way. Muscles remain plastic in adulthood and can self-repair. Muscles are intimately tied to pressure in the fluid system that supports them. Muscles are involved in metabolic regulation and can even serve as a source of fuel in starvation. Finally, muscles are obviously not the only part of an animal that makes spectacular performances possible. We must understand what muscle uniquely contributes to an integrated, tuned system that includes multiple muscles, joints and sensors, a transport system for fuel delivery, and a complex control system, all of which functions through skeletal scaffolding.

To design an artificial muscle is a worthy endeavor. However, we strongly urge that nature's technologies provide biological inspiration for artificial technologies. Biological inspiration should involve the transfer of principles or lessons discovered in a diversity of animals. Our knowledge of biological muscle should be able to assist us in the construction of an actuator with desired performance capacities only observed in animals. However, the performance of biological actuators should not be and has not been the single design by which we measure our success. We have and will continue to design human-made actuators that exceed natural muscle in performance in particular metrics and for specific tasks.

If we are to call a human-made actuator an artificial muscle, we must detail precisely the tasks that uniquely define what muscles do. Metrics can best be *compared* under common conditions. To develop these appropriate tests is an ongoing challenge, because we are still discovering how muscles work in animals. Moreover, engineers have a multitude of metrics that have made relevant, direct comparisons nearly impossible. The design of an artificial muscle will require novel interdisciplinary collaborations between muscle biologists and engineers. Biologists can provide inspiration and detail about what is known at present, but engineers can reciprocate with quantitative hypotheses and novel instrumentation that will lead to new tests and discoveries of muscle function.

With these important caveats declared, this chapter serves as a guide through some of the classical metrics of muscle function that can allow comparisons.

3.2   Common Characterizations—Partial Picture

3.2.1   Maximum Isometric Force Production Depends on the Level of Neural Activation

The maximum force an active muscle can generate is most often measured at a set length when muscles are not allowed to shorten. This type of contraction is termed isometric. The force generated by muscle during an isometric contraction is a function of neural activation (Fig. 1). Single neural stimuli produce small, transitory increases in force called twitches. Consecutive stimuli in the form of a train of neural spikes lead to a summation in force. Maximum, sustained isometric force can be attained at the greatest stimulation frequencies when the muscle is in tetanus. Maximum force increases with the cross-sectional area of the muscle stimulated. Values of maximum isometric stress vary by over 100-fold and range from 0.7 to 80 Ncm^{-2} [Full, 1997; Josephson, 1993]. In general, force development tends to be the greatest in the slowest muscles.

3.2.2   Rate of Force Production and Relaxation Varies Among Muscles

The rates of muscle force generation and relaxation are important because they reveal possible limitations to duty cycles required for rhythmic activity. Slow kinetics can limit behavior if antagonistic muscles co-contract. Muscles operating in escape or producing small strain vibrations such as the insect flight muscle and the rattlesnake shaker muscle demonstrate the fastest kinetics [Rome, 1998]. Reported contraction times to peak force vary by over 200-fold. Values range from 0.004 to 0.79 sec, but the lack of standardization of conditions makes direct comparison difficult [Full, 1997]. Time to 50% relaxation varies by over 100-fold and ranges from 0.009 to as long as 1.1 sec.

3.2.3   Maximum Isometric Force Depends on Muscle Length

The magnitude of a muscle's isometric force development depends on the length at which it is set (Fig. 2). Active muscle force is reduced at the shortest and longest muscle lengths because of the filamentous nature of the contractile structure. Maximum, active isometric force is attained at intermediate muscle lengths. Animals tend to operate on the ascending part of the active force-length curve. It is important to note that passive muscle force increases curvilinearly at longer muscle lengths where active force declines. As a consequence, total muscle force can increase at longer muscle lengths.

Active force-length curves vary in the degree to which force decreases with changes in length (Fig. 3). The largest differences are seen when flight muscle is

compared to the body-wall muscle of animals that crawl using hydrostatic skeletons, like insect larvae [Full, 1997]. Flight muscle can only generate maximum force over a very narrow range of strain (2 to 4%) as these muscles appear to simply vibrate. By contrast, body-wall musculature of soft-bodied animals operates over a large range of length changes (200%) corresponding with the considerable shape changes in these species.
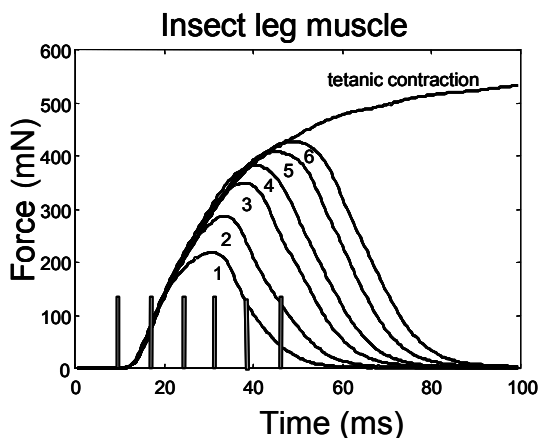

Figure 1: Force produced by activation of a muscle. Force production of a cockroach muscle (muscle #177c) increases as a function of the number of input pulses.
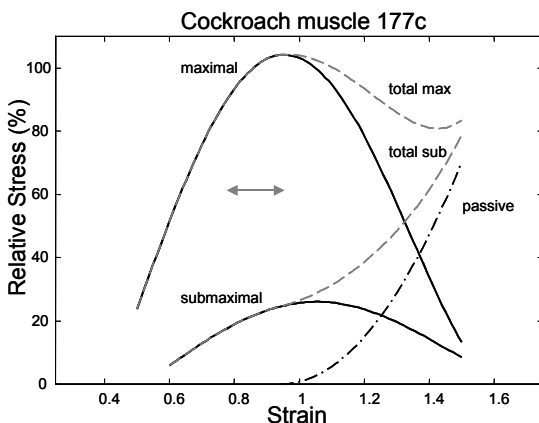
Figure 2: Strain-stress characteristics of maximally and submaximally activated cockroach muscle (#177c; represented by continuous lines) as well as the passive length-force characteristics (dashed-dotted line). Total muscle force is equal to the sum of active and passive force (represented by gray dashed lines). Stress is normalized to the peak isometric tension. Strain is normalized as a fraction of the length that gives peak isometric stress. The arrow indicates range of strains where muscle functions under natural conditions.

Figure 3: Active length-force or strain-stress curves. Stress is normalized to the peak isometric tension. Strain is normalized as a fraction of the length that gives peak isometric stress. Shaded areas represent st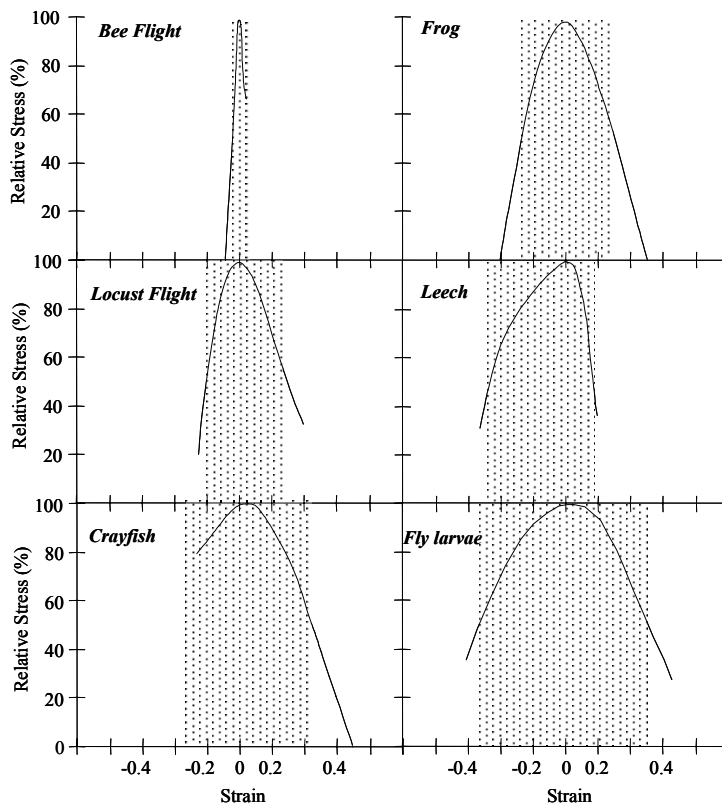rains that correspond to stresses above 50% maximum isometric stress. Data include bee flight, locust flight, crayfish, frog, leech, and fly larvae muscle [Full, 1997].

3.2.4 Force Development Decreases with an Increase in Shortening Velocity

The faster a muscle shortens, the less force it can develop (Fig. 4). Said in another way, when muscles have larger loads, they contract more slowly. Single contractions of maximally activated muscle are studied by measuring either force or velocity, while holding the other constant. These are referred to as isotonic or isovelocity contractions. Data from frog, rat, turtle, fish, locust, beetle, and scallop muscle all show the characteristic rectangular hyperbolic shape with force decreasing with an increase in velocity [Full, 1997; Rome and Lindstedt, 1997; Josephson, 1993]. The maximum shortening velocity of muscles varies both within an individual and among species. Maximum shortening velocity varies by over 50-fold, ranging from 0.3 to 17.0 lengths/sec depending on the slowest

muscle of a hydrostat selected for inclusion [Full, 1997; Josephson, 1993]. The force-velocity relationship for lengthening contractions is less well defined [Josephson, 1999] (Fig. 4). However, when muscle is stretched, the force developed often exceeds that of maximum isometric force by nearly twofold.
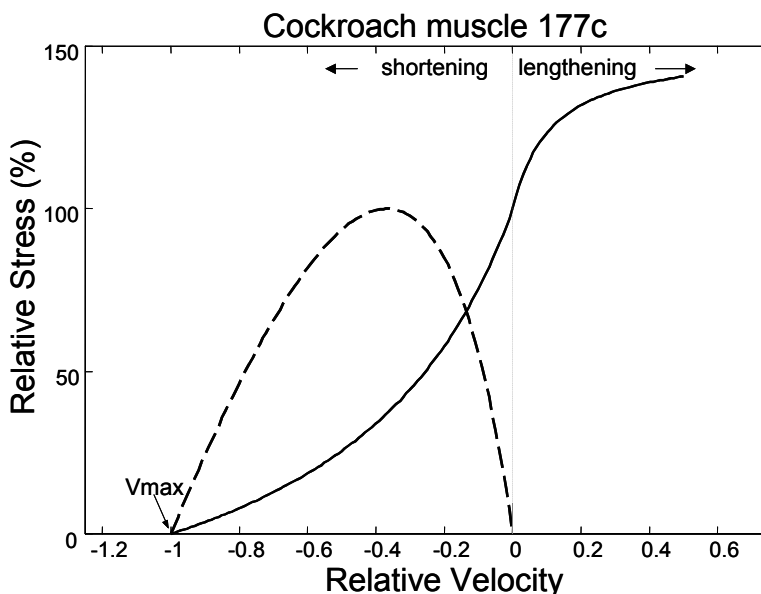

Figure 4: The force-velocity curve for active cockroach muscle (continuous line). Stress is normalized to the peak isometric tension. Velocity is normalized as a fraction of the maximal shortening velocity of the muscle (V_{max} = the highest velocity at which the muscle can still generate force). Force is larger than the isometric force if the muscle is lengthening and lower than the isomeric force when the muscle is shortening. The instantaneous power (force $\times$ velocity) is represented by the dashed line.

3.2.5 "Blocked Stress" Calculations Overestimate a Muscle's Capacity to do Work

Work and power output of a muscle can be bounded from the metrics thus far mentioned. The product of maximum force and length change can yield an estimate of maximum work output [Wax and Sands, 1999]. This blocked stress value can be misleading for several reasons. First, the maximum force produced by muscle does not necessarily occur in the same muscle that produces the largest changes in length. Second, because force is a function of velocity, maximum work and power output for single contractions occur at approximately one-third of maximum velocity. Third, although work and power output for single contractions can be estimated from the force-velocity relationship for a

single contraction, they overestimate the work and power of muscles operating in animals [Josephson, 1989]. Muscle physiologists sometimes refer to these estimates as instantaneous work and power. Because most activities involve cyclic contractions, muscle is inactive for nearly one half a cycle. Instantaneous work and power estimates can exceed what muscles are capable of by twofold.

Next we discuss the method now used by muscle physiologists interested in understanding how muscles function during activity in animals. Examining rhythmic activities has shown not only that we need to be cautious about our comparisons of work and power, but that discoveries have revealed that muscle has more diverse roles.

3.3 Work-Loop Method Reveals Diverse Roles of Muscle Function during Rhythmic Activity

Muscles are used by animals in rhythmic activities such as running, swimming, flying, chewing, and communicating. Cycle frequency, level and pattern of neural stimulation, phase of neural stimulation, strain pattern, and magnitude are required to define the workspace for muscles undergoing rhythmic oscillations. A technique referred to as the "work-loop method" allows a muscle physiologist to control each of these parameters. Using this technique, muscle is attached to a moveable lever, subjected to cyclic length changes, and stimulated at a distinct phase in its motion, while muscle force is measured [Josephson, 1985] [Fig. 5(a)]. From muscle force and length changes, a work-loop is created. Net work equals the work done during shortening minus the work done during lengthening [Fig. 5(b)]. If the shortening or positive work exceeds the lengthening or negative work, then energy is generated by the muscle (positive, counterclockwise loop for stress vs. strain). If the positive work is less than the negative work, then energy is absorbed by the muscle (negative, clockwise loop).

Muscle physiologists, thus far, have used the work-loop technique in at least two ways. First, by varying the controlled parameters, we have searched for a muscle's maximum capacity to do work and generate power. Second, we have input the parameters actually used by an animal during an activity. An advantage of the work-loop method is that the stimulation pattern used by the animal can be better approximated [Dickinson et al., 2000]. The stimulation pattern, magnitude and phase selected by an animal during an activity can be determined from electromyograms (EMGs), and then later played back into the motorneuron, stimulating the muscle attached to the lever. In addition, muscle strain can be estimated from joint kinematics or measured directly in a freely moving animal by sonomicrometry [Biewener et al., 1998a, b]. Strain patterns can be programmed into the lever attached to the muscle to mimic length changes measured in the animal during a behavior in nature.

We first discuss the results from work-loop experiments conducted by muscle physiologists searching for maximum power output and the parameters that produce it. Following this, we show examples of how muscles function when we use the parameter values that animals select in nature.
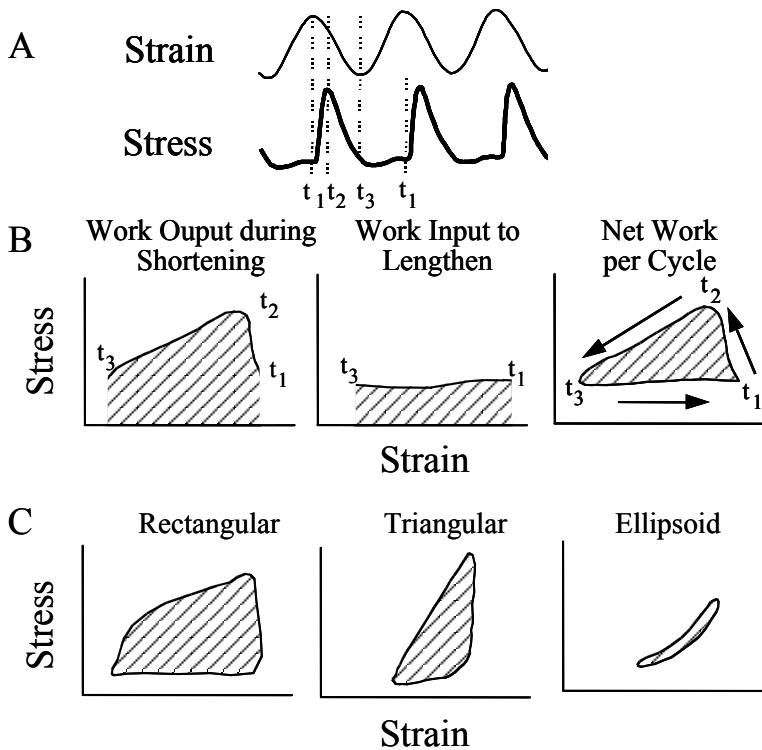
Figure 5: Schematic representation of the work-loop technique. (a) Muscle stress and strain patterns for three cycles. (b) From left to right, the work done by the muscle on its environment, the work done on the muscle and the resulting net work output. (c) Different kind of work loops that are found for different muscles [after Josephson, 1985]. (Courtesy of The Company of Biologists Ltd.)

3.3.1 Work-Loop Method Provides Better Estimate of Maximum Power Output during Rhythmic Activity

Single isotonic or isovelocity contractions do not mimic muscle function in most animals. Propulsive units most often function rhythmically. Instantaneous power output estimates do not consider the frequency of cyclic movement nor do they mimic the neural stimulation pattern in animals. As a result, instantaneous muscle power output (the product of force and velocity from the force-velocity relationship) overestimates power output of a propulsor by two- to threefold because muscles in an animal are usually not generating power for half or more of the cycle. Muscles rarely shorten at a constant force or velocity during activity, but lengthen and shorten in a more sinusoidal fashion [Johnston, 1991; Josephson, 1985]. Muscle force or stress varies with phase of activation, strain,

and frequency. Imposing sinusoidal length and velocity changes on muscle reduces maximum power output estimates by as much as 20% compared to estimates assuming linear or constant velocity shortening. A survey of work-loops yielding maximum power output shows that work-loop shape depends on the frequency of operation and seldom results in a shape comparable to the perfect rectangle assumed by a "blocked stress" estimation [Fig. 5(b)].

3.3.2   Mass-Specific Work Output Decreases with Cycle Frequency

From data on oscillatory contractions, muscle mass-specific, work output ranges from 9 to 284 W/kg [Altringham et al., 1993; Askew and Marsh, 1997; Biewener et al., 1998b; Couglin, 2000; Ettema, 1996; Girgenrath and Marsh 1999; Full, 1997; Hammond et al., 1998; James et al., 1995, 1996; Prilutsky et al., 1996; Rome et al., 1999; Swoap et al., 1993]. Mass-specific muscle work per cycle that yields maximum power output decreases with an increase in frequency (Fig. 6). The decrease in work results from a decrease in stress (five-fold for a 100-fold change in frequency) and strain (six-fold decrease; Fig. 7). Strain rate at maximum power output increases by 16 fold with a 100-fold increase in muscle cycle frequency. In addition, the shape of the work-loop changes [Fig. 5(c)]. Work-loops tend to be more rectangular at low frequencies (< 30 Hz). Higher forces are attained by using multiple stimuli. Work-loops are more triangular shaped at intermediate frequencies (~30–60 Hz). The forces measured often result from twitches generated by one or two stimuli per cycle. At the highest frequencies (~60–180 Hz) work-loops are ellipsoid and more springlike.

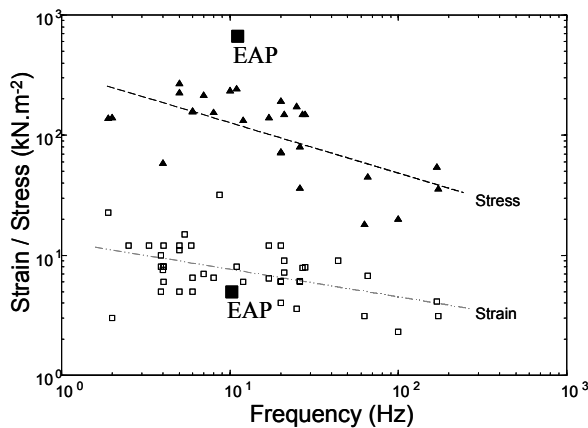**Figure 6:** Mass-specific muscle work per cycle as a function of frequency for vertebrate and invertebrate muscles (open circles). Data were obtained using the workloop method [Josephson, 1985]. (Courtesy of The Company of Biologists). Preliminary results show that EAPs fall within the range of values for natural muscle [Full, 1997]. [By permission of Oxford University Press (www.oup.com).**]**
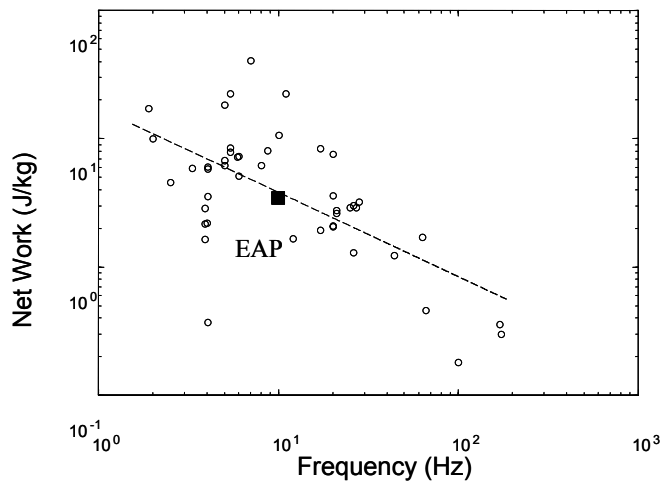
Figure 7: Stress (filled triangles) and strain (open squares) of vertebrate and invertebrate muscle as a function of frequency. Data for EAP muscle is represented by filled square [Full, 1997]. [By permission of Oxford University Press (www.oup.com).]

3.3.3 Mass-Specific Power Output is Independent of Cycle Frequency

Maximum, mass-specific, power output ranges from 9 to 284 W/kg in animals as diverse as birds, cats, rats, mice, bees, fish, crabs, and scallops [Full, 1997]. Maximal, mass-specific power appears to change little with frequency or body mass (Fig. 8). The decrease in stress, strain and work observed as frequency increases is balanced by the increased frequency, since power output is the product of stress, strain, and frequency.

3.3.4 Work-Loop Method Shows Muscles have a Role in Energy Management and Control

Although a muscle may be capable of generating substantial amounts of power under certain conditions, muscles can play different roles for particular behaviors in nature [Dickinson et al., 2000]. For example, an insect leg muscle is capable of generating power at low strains if stimulated slightly before leg extension. During wedging or pushing underneath an object, the muscle does indeed operate in this space [Full and Ahn 1995]. However, during running, the same muscle is subjected to large strains, produces clockwise work-loops, and therefore, only absorbs energy to control the swing of the leg [Full et al., 1998] (Fig. 9). Similarly, control muscles of flies generate little or no mechanical power, because they function as tunable springs to direct the forces of much larger
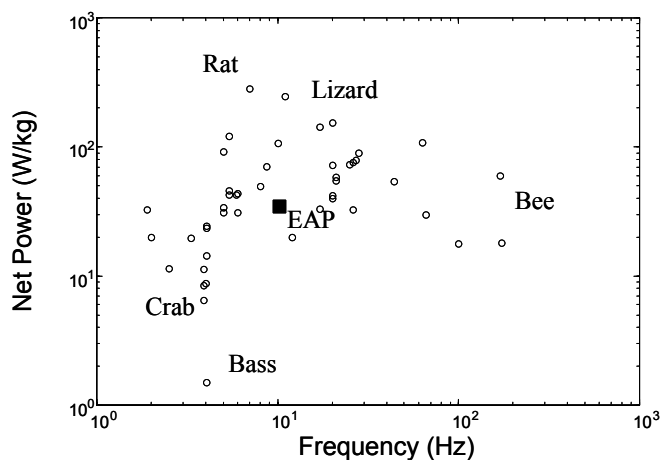
Figure 8: Mass-specific power output of muscles [Full, 1997; Josephson, 1993] (circles) and an electroactive polymer (filled square) as a function of the frequency of oscillation. Data were obtained using the work-loop method [Josephson, 1985]. Preliminary results show that EAPs fall within the range of values for natural muscle. (Courtesy of Oxford University Press (www.oup.com), Annual Review of Physiology, and The Company of Biologists.)

power muscles, thus allowing the nervous system to rapidly change wing kinematics by varying the timing of activation. Whereas the large pectoralis muscle of a bird powers flight, another controls joint stiffness, and may modulate wing shape during takeoffs and turns [Dial, 1992]. The axial muscles of fish can serve as either force-generators or energy-transmitters, depending on when they are activated with respect to the undulatory wave that passes along the body. In eels, muscles all along the trunk may contribute to the generation of mechanical power [Gillis, 1998]. In fish that generate the bulk of their hydrodynamic forces using their tail fin, anterior muscles generate energy that is transmitted to the fin through the stiffening action of more posterior muscles.

By measuring both the length and force of a muscle in an active animal at the same time, it is even possible to calculate in vivo work-loops. Direct measurements of muscle length changes in behaving animals have been obtained using sonomicrometry, whereas forces have been measured with strain gauges attached to tendon buckles or to the wing bones of flying birds [Biewener et al., 1998]. In running turkeys and hopping wallabies, muscle fiber length remains nearly constant or even shortens while the tendon stretches [Roberts et al., 1997; Biewener et al., 1998]. Under these conditions, muscles act as struts, permitting the elastic tendons to store and release energy. Examples of multifunctionality and division of labor are likely to become increasingly common as more muscles are measured.
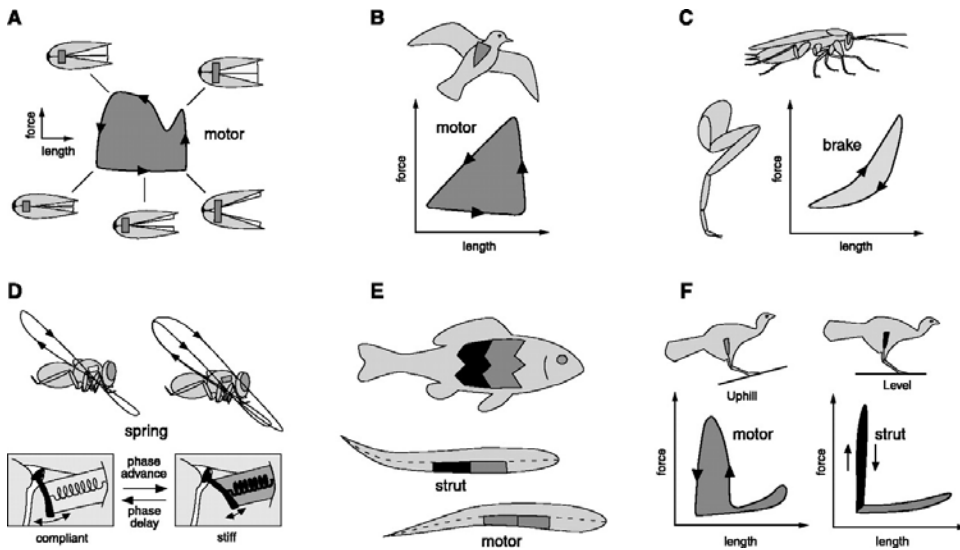
Figure 9: Muscles can act as motors, brakes, springs, and struts. Muscles that generate positive power (motors) during locomotion, and the area within associated work loops, are indicated in red. Muscles that absorb power during locomotion (brakes), and the area within associated work loops, are indicated in blue. Muscles that act as springs of variable stiffness are indicated in green. Muscles that act to transmit the forces (struts) are shown in black. (a) Scallop swimming provides a simple example of a muscle generating positive work to act as a motor [Marsh and Olson, 1994]. (b) The pectoralis muscle of birds generates the positive power required to fly [Biewener et al., 1998b]. (c) In running cockroaches, some muscles that anatomically appear to be suited for shortening and producing power, instead act as brakes and absorb energy because of their large strains [Full et al., 1998]. (d) In flies, an intrinsic wing muscle acts to steer and direct the power produced by the primary flight muscles [Tu and Dickinson, 1996]. (e) In swimming fish, the function of muscles varies within a tail-beat cycle. In some fish designs, early in a beat, the cranial muscle fibers shorten and produce power that is transmitted by more caudal muscle fibers acting as struts. As the beat continues, the fibers that were previously acting as struts change their role to power producing motors. The image at the top shows a fish from the side. Beneath it are shown views from above the fish at two points in the tail-beat cycle [Altringham et al., 1993]. (f) In vivo muscle force and length measurements in running turkeys indicate a dual role for the gastrocnemius muscle. It generates positive power during uphill running, but acts as a strut during level running, which allows the springlike tendons to store and recover energy [Roberts et al., 1997]. (Reproduced with permission from Dickinson et al. [2000]. Courtesy of the American Association of the Advancement of Science.)

3.4 Direct Comparisons of Muscle with Human-Made Actuators

A wide range of materials with musclelike properties are currently available or being developed [Wax and Sands, 1999]. Their properties vary considerably, particularly with respect to the stress, strain, operation frequency, and power output that they can attain. Each material appears to have particular advantages for certain types of activities. Appropriate evaluations of these actuators are most often made with a particular application in mind. In many cases, these evaluations have made a direct comparison to biological muscle difficult. We propose to begin mapping the properties of presumed artificial muscle to the workspace of natural muscle. One way to achieve this goal is to test the proposed artificial muscles in the *same apparatus* with the *same methodology* with which natural muscle is most effectively evaluated. Few studies have compared the mechanical properties of artificial and natural muscles directly [Gonzalez et al., 1997; Klute et al., 1999] and to our knowledge no study has addressed such a comparison from the perspective of muscle function within an animal.

3.4.1 Evaluating Musclelike Properties of Electroactive Polymers (EAPs) Using the Work-Loop Technique

In collaboration with SRI International, we are currently measuring the musclelike properties of electroactive polymer (EAP) actuators [Meijer et al., 1999]. We have examined EAP actuators in the very same experimental apparatus in which we test natural muscle (Fig. 10). The muscle lever system can simultaneously vary actuator length; control the intensity and phase of stimulation; and record position and force. With this system we used the work-loop technique to determine power output.
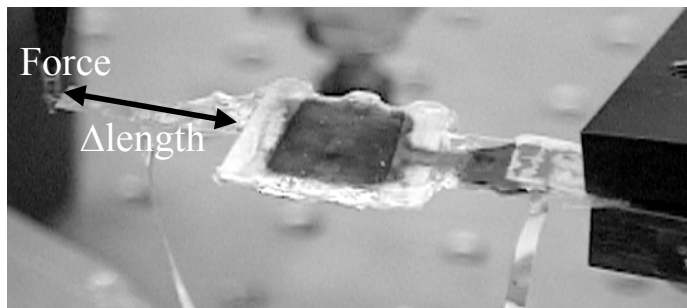

Figure 10: Acrylic dielectric elastomer actuator (black square area in middle of picture) from SRI International in lever setup used for muscle experiments. The black arrow indicates the length changes that were imposed on the actuator by the muscle lever. Force was recorded at the left tip of the actuator [Meijer et al., 1999]. (Courtesy of Knowledge Press.)

3.4.2   Activation, Stress, and Strain during Cyclic Activity

As in natural muscle, the force production of EAPs varied with the level of stimulation. EAPs, however, require stimulation for relaxation. We have not yet determined the ramifications of this difference with respect to energy consumption nor have we explored the necessary difference in control or connections to skeletal structures. Preliminary results show that the maximum stress attained by EAPs (~80 Ncm^{-2}) falls above the range of values measured for natural muscle. The strain at which the EAPs produced maximal power (2.5%) is at the lower end of the range of values measured for natural muscle (Fig. 7). The EAPs are capable of much higher (> 100%) unloaded strains [Pelrine et al., 2000].

3.4.3   Mass-Specific Power Output of an EAP can Fall within the Range of Natural Muscle

The EAP actuator was capable of both generating and absorbing energy much like natural muscle. When the actuator was stimulated during the lengthening phase of the cycle it overcame the viscoelastic losses of the material and generated power. We obtained a maximal power output of 40 W/kg at a cycle frequency of 10 Hz, a strain of 2.5% and a stimulation voltage of 6 kV. Our preliminary results show that the power output of EAPs falls within the boundary of values for natural muscle when near maximal activation.

3.5   Future Reciprocal Interdisciplinary Collaborations

Natural muscles differ greatly in capacity among animals that crawl, climb, burrow, walk, run, jump, glide, fly, swim, skate, and sing [Full, 1997; Rome and Lindstedt, 1997; Johnston, 1991; Rome, 1998]. Muscles differ both in their fundamental properties as well as how animals use the muscles in nature. Muscles perform in a variety of ways during animal activities. In some cases, muscles and their attachments are primarily force generators used for stabilization and support of limbs and skeletons, allowing for the possibility of springlike function [Biewener 1998]. In other cases, muscles function to produce the rapid movement of limbs or body parts. Most often muscles both generate and absorb energy. These diverse roles of muscle function were discovered using the work-loop technique, but required a directed effort toward understanding how muscles function in the whole animal. To best understand the capabilities of an artificial muscle, it may require building an array of devices within which the artificial muscle may function.

   We strongly urge a common standard for direct comparisons between natural and artificial muscle. To call an actuator musclelike, its capabilities should fall within the functional space of natural muscle. No matter what the standard or evaluation technique used for human-made actuators, we recommend more communication between muscle physiologists and engineers in the future.

3.6 Acknowledgments

3.7 References

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