The design of the muscular system

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Abstract Animals produce a wide range of movements, both fast ones and slow ones. Many parameters in the muscular system (maximum velocity of shortening [V_{max}], gearing of fibers, kinetics of activation and relaxation, myofilament lengths) show considerable variation. Our goal has been to determine the rules (design constraints) which govern what values these parameters have in a given animal. By a combination of whole animal measurements during locomotion (sarcomere length [SL] changes, muscle shortening velocity [V], and fiber recruitment) and isolated muscle mechanics measurements (V_{max}, SL-tension relationship), we have found evidence for two constraints in the design of the muscular system. Parameters appear to be set so that 1) active fibers operate over optimal myofilament overlap (where maximum tension is generated) and 2) active fibers shorten at V/V_{max}'s of 0.17-0.38 (where maximum power and optimal efficiency are obtained). A given animal produces a wide range of movements while its active fibers obey these constraints, by recruiting different fiber types that have different V_{max}'s and different gearing (Δ body movement/Δ SL). Because different fiber types also have different metabolic capabilities, these mechanical constraints have important implications for neuromuscular fatigue.

One of the most fascinating areas of physiology is the study of how parameters of a given system are fine-tuned to provide optimal performance under a variety of conditions. The components that make up the muscular system are fairly well understood and some show tremendous variation. It seems reasonable that evolution has set the values of various parameters to enable animals to locomote over a wide range of speeds efficiently.

Although we know what the important components are and how they vary, we do not know how the system is designed. An understanding of how the muscular system is designed requires us to understand how the various components are integrated into the system, or more specifically, given the variation that occurs in each component, by what rules does evolution choose the values for each parameter.

Over the past seven years, my laboratory has performed both isolated muscle and whole animal experiments in a effort to elucidate (1) whether there are identifiable rules by which values for various components of the system are set to enable animals to perform the wide range of activities that a given animal performs and (2) whether or not these rules hold for the great variety of locomotory behaviors in which vertebrates engage.

From cell physiology, we may anticipate that there are some rules (Fig.1) that are followed when an animal muscular system is designed. During steady activation, the force muscle generates depends on the amount of overlap between myosin and actin filaments, or more precisely, the number of myosin crossbridges which can interact with actin sites (Gordon et al.1966). It would seem sensible for animals to vary the gear ratio of their muscle fibers and their myofilament lengths, so that no matter what movements the animal makes, the muscle would operate at optimal myofilament overlap (i.e. where the muscle generates near maximal force). As such, gear ratio and myofilament lengths can be viewed as the design parameters (those components that can be varied during evolution). Myofilament overlap can be viewed as a design constraint or design goal (i.e., what has to remain constant or the rule by which the variation in parameters is adjusted). As both design parameters are anatomical features of the muscle, one at the organ level and the other at the molecular level, this can be viewed as a structural design consideration.

There is also a dynamic design consideration which takes into account that muscle shortens

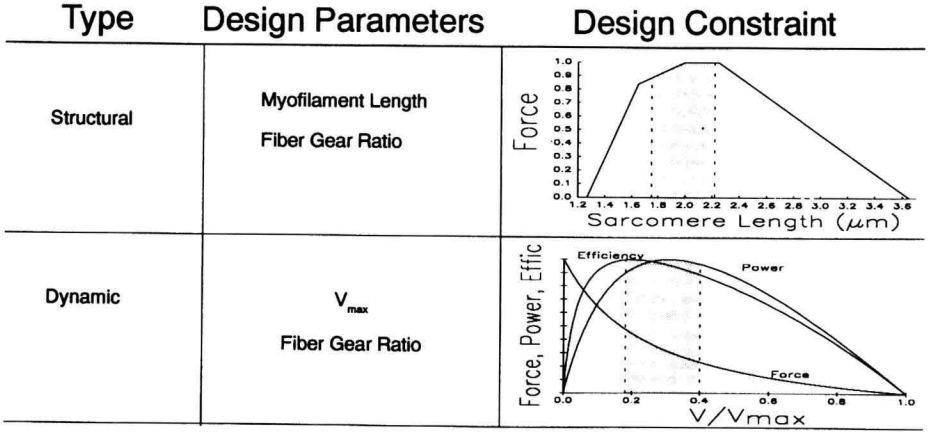

Figure 1. Steady state design constraints. Our empirical studies suggest that myofilament overlap and V/V_{max} are important design constraints, that is, the rules by which the values of design parameters are set.

during locomotion. The force muscle generates is a function of V/V_{max}. More importantly, the mechanical power that a muscle generates and the efficiency with which it generates the mechanical power are functions of V/V_{max} as well. Again, we might anticipate that the muscular system would be designed so that no matter what movement the animal makes, the active fibers operate over a range of V/V_{max} values (0.15 - 0.40), where the fibers generate maximal power at maximum efficiency. Thus, the design parameters V_{max} and fiber gear ratio are varied in such a way that they operate under the design constraint of V/V_{max}.

Different types of animals face very different problems during locomotion and hence, their muscles must perform different activities. Because the potential design constraints listed above formally refer only to shortening contractions (as opposed to isometric or lengthening contractions), our research to test these design constraints has focused on animals which primarily use shortening contractions (fish and frogs).

I. Design Constraint #1 - Myofilament overlap

The simplest design constraint is myofilament overlap (the SL-tension relationship). Because of the sliding filament structure of muscle, muscle generates maximum force over a fairly narrow range of SLs (Gordon et al.1966). Researchers have assumed that the muscle is used only over those SLs, but there has been relatively little evidence to justify this assumption.

Our recent experiments on carp provide the most extensive study of these issues. To swim, a fish must bend its backbone. By a combination of high speed motion picture and anatomical approaches, we have found that at low swimming speeds, the red muscle (Fig. 2), which powers this movement, undergoes cyclical SL excursions between 1.89 to 2.25 μm centered around a sarcomere length of 2.07μm (Rome et al.1990a). Further, we determined from electron microscopy that thick and thin filament lengths of the red (1.52μm and 0.96μm) and white (1.56μm and 0.99μm) muscle in carp are similar to that in frogs (Sosnicki et al.1991). Using the frog SL-tension relationship, the red muscle was shown to be operating over a range of SLs where no less than 96% maximal tension is generated (Rome and Sosnicki, 1991).

We then examined the most extreme movement carp make, the escape response. This involves a far greater curvature of the backbone than steady swimming. If the red muscle were powering this movement, it would have to shorten to a SL of 1.4 μm where low forces and irreversible damage can occur (Fig 2c; Rome and Sosnicki, 1991). Rather it is the white muscle which performs the movement, because the white muscle has a different orientation than the red. The red muscle fibers run parallel to the long axis of the fish just beneath the skin (Fig. 2a). The white muscle fibers on the other hand, run in a helical orientation with respect to the long axis of the fish. We have empirically shown that the helical pattern

endows the white muscle with the a 4-fold higher gear ratio (Δ backbone curvature/ΔSL).

Thus, for a given backbone curvature, the white muscle undergoes only about 1/4 the SL excursion of the red. To power this most extreme movement of fish, in the worst case (posterior), the white muscle must shorten to a SL of 1.75μm (Fig. 2c). At this SL the muscle generates about 85% maximal force. Most of the volume of the white muscle (middle and anterior sections), however, does not shorten as much and thus generates even more force (95% for anterior and 92% for the middle). When the white muscle is used in less extreme movements (i.e., during fast swimming), the curvature of the backbone is not nearly as severe, and thus the white muscle generates nearly maximal force (Rome and Sosnicki, 1991).

As we have shown above, the myofilament overlap is never far from its optimal level even in the most extreme movements. It appears, therefore, that animals are designed in such a way that no matter what the movement, the muscles used generate nearly optimal forces. As such, myofilament overlap can be considered a design constraint (i.e., an aspect of the system that is kept constant). Given the movements that animals need to make, two design parameters (fiber orientation and myofilament lengths) are adjusted during evolution such that the active fibers always operate at near maximal myofilament overlap and force generation (Fig. 1).

To test this design constraint further, we examined frog jumping. It seemed that in an all-out movement like a frog jump, a good strategy might be to circumvent (to some extent) this constraint and for the frog to passively stretch the sarcomeres to long lengths in its crouching position. Hence, instead of being restricted to small SL excursions (as in fish), the sarcomeres could shorten up the descending limb, through the plateau, onto the shallow ascending limb, providing a longer SL change (stroke) and produce more work.

Lutz and Rome (1991) have recently shown on two hip extensor muscles (gracilis and semimembranosus) that frogs in fact do this. During a jump, both muscles shorten from a resting sarcomere length of ~2.6μm down to ~2.0μm. Over these SL's the muscle would generate no less than 75% maximum force. However, at the point in the jump when the frog is generating maximum power (~2.38 μm), the force would be no less than 91%. These results further support the theory that myofilament overlap is a design constraint in muscular systems, although it is a slight variation on the theme evidently adapted for jumping.

II. Design Constraint #2-V/V_{max}

V_{max} can vary greatly. Differences in V_{max} have been found in a given muscle at different temperatures, in different muscle fiber types within the same muscle, and in muscles from different animals. To a first approximation, fibers with different V_{max}'s generate the same maximum isometric force per cross-section and have the same maximum efficiency, whereas the maximum power generated and rate of ATP splitting in the fiber with a high V_{max} is considerably greater than in the fiber with a low V_{max} (Fig. 3).

From Hill's work (Hill, 1938), we know, however, that a muscle fiber's mechanical properties (force generation and power production) and energetic properties (ATP utilization and efficiency) are not simply a function of the fiber's V_{max}. They also depend on V/V_{max}.

Figure 3 shows the force, power output, and efficiency of fibers with 2 different V_{max} values. For a given V, the force and mechanical power per cross sectional area can be considerably higher in the fiber with a high V_{max} (at V_1, they are similar, whereas at V_2, they are quite different; Fig. 3a,b). It would thus seem advantageous to only have muscle fibers with high V_{max}'s. There is, however, an energetic price paid for a high V_{max}. The rate of ATP utilization in the fiber with a high V_{max} is considerably greater than in a fiber with the low V_{max} at all velocities of shortening. Thus, there appears to be an adaptive balance between the mechanics and energetics of contractions. The fibers with low V_{max} are more efficient at low V (e.g. V_1). At higher velocities (e.g. V_2), however, the fibers with high V_{max} are more efficient (Fig 3c). Thus, to produce both slow movements and fast movements efficiently, the animal should use the fibers whose V_{max} is matched to the V at which it needs to shorten.

If V/V_{max} is in fact a design constraint we would anticipate that a given muscle fiber type would be used over a range of V/V_{max} of about 0.15 to 0.40 where efficiency and power output are maximal. Thus the two design parameters, V_{max} and gear ratio, should be set so that during all body movements, the V falls within this range of V/V_{max} (as in Fig. 1).

To determine V/V_{max} one must determine (1) which muscle fibers are active during a given activity, (2) the V at which the fibers shorten (i.e, slope of the SL-time graph), and (3) the V_{max} of the different fiber types. It is the first of these measurements which led us to work on

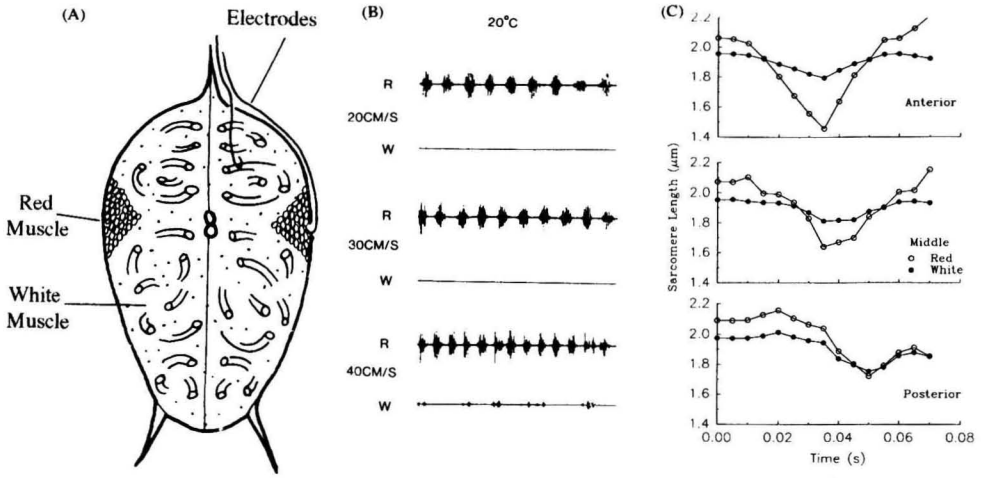

Figure 2. Cross-sectional view of carp (a). The red muscle forms a thin sheet just under the skin (its thickness is exaggerated for illustrative purposes). The red fibers run parallel to the body axis (i.e., out of the page). The white fibers run in a helical fashion with respect to the backbone. Consequently, they need shorten by only ~1/4 as much as the red ones to produce a given curvature change of the body. Placement of electromyography (EMG) electrodes are shown. EMGs from red (R) and white (W) muscle of carp at 20°C (b). The SL excursions of the white muscle in the anterior, middle and posterior positions during the startle response (c). Note that the red fibers do not actually shorten to the SL shown because they cannot shorten fast enough. Adapted from Rome et al. (1984,1988) and Rome and Sosnicki, (1991).

fish. Because of the anatomical separation of their different muscle fiber types (Fig 2a), it is possible to monitor activity of different fiber types by EMG. For instance, we know from EMGs at slow speeds that only the red fibers are active, and at fast speeds the white muscle fibers are recruited as well (Fig. 2b).

To test the importance of V/V_{max} as a design constraint, we have examined this parameter in four situations. Each situation was chosen to change either the numerator, V, or the denominator, V_{max}, in order to see if there was a concomitant change in the other parameter to maintain a constant V/V_{max}.

A. Different Fiber Types in Carp

The first question we asked is why animals have different fiber types (i.e., different V_{max}'s within the same animal). Are the faster fibers used for faster movement (higher V's) so that they operate at the same V/V_{max}? As illustrated in Fig. 3, the V_{max} of carp red muscle was 4.65 muscle lengths/s (ML/s) and the V_{max} of carp white muscle 2.5 times higher, 12.8 ML/s (Rome et al.1988). During steady swimming the red muscle is used over ranges of velocities of about 0.7 to 1.5 ML/s (shaded portion of Fig. 3d). This corresponds to a V/V_{max} of 0.17-0.36, where maximum power is generated. At higher swimming speeds (higher V's) the fish recruited their white muscle because the mechanical power output of the red muscle declines.

It is clear from Fig. 3d, that red muscle cannot possibly power the escape response. To power the escape response, the red muscle would have to shorten at 20 ML/s, which it clearly cannot do, as this is 4 times its V_{max}. But even if the white muscle were placed in the same orientation occupied by the red (i.e., same gear ratio), it couldn't either, because its V_{max} is only about 13 ML/s. However, because of its 4-fold higher gear ratio, the white muscle need shorten at only 5 ML/s to power the escape response (Fig. 3), which corresponds to a V/V_{max} of about 0.38, which is where white muscle generates maximum power.

Thus the red and white muscle form a two gear system which powers very different movements. The red muscle powers slow movements, while the white muscle powers very fast movements, both while working at the appropriate V/V_{max}. In terms of backbone curvature, the white muscle can produce 10-fold faster movements (2.5-fold higher V_{max} x 4

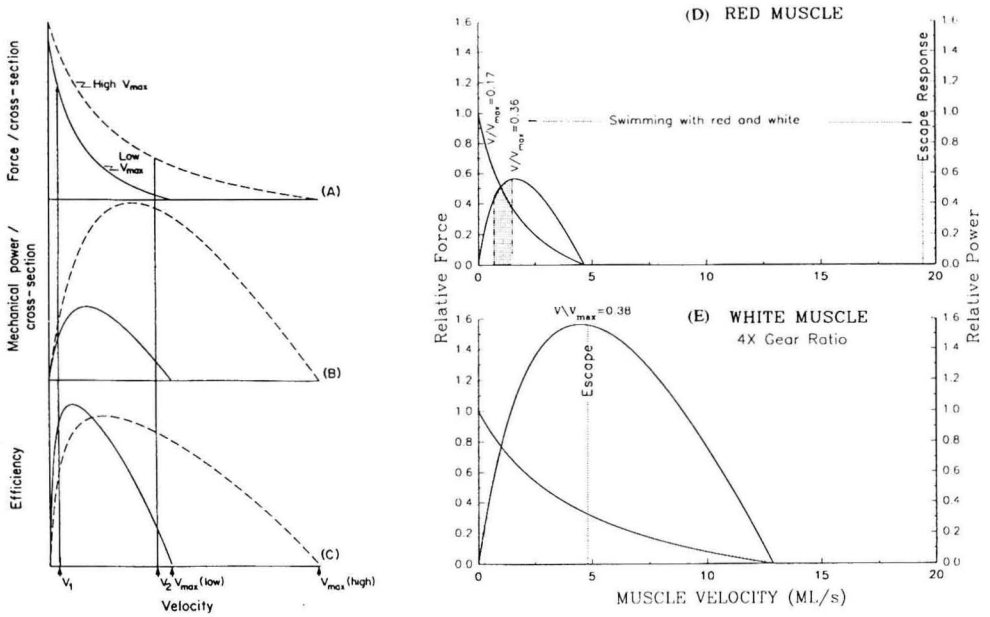

Figure 3. Relative force (a), power (b), and efficiency (c) as a function of relative shortening velocity for a muscle with a high $\mathbf{V_{max}}$ (dashed curves) and a muscle with a low $\mathbf{V_{max}}$ (solid curves). V_1 and V_2 are arbitrarily chosen examples of low and high shortening velocities. Design constraint #2--$\mathbf{V/V_{max}}$ (d,e) During slow movements and fast ones the active fibers always shorten at a $\mathbf{V/V_{max}}$ of 0.17-0.38 where maximum power and efficiency are generated. During steady swimming (red muscle), the fibers are used at a $\mathbf{V/V_{max}}$ of 0.17-0.36 (d). The red fibers cannot power the escape response because they would have to shorten at 20 ML/s. The escape response is powered by the white muscle which need shorten at only 5 ML/s ($\mathbf{V/V_{max}}$ =0.38) because of its 4X higher gear ratio (e). The white muscle would not be well suited to power slow swimming movements, because it would have to shorten at too low a $\mathbf{V/V_{max}}$ (0.01-0.03; adapted from Rome 1990,1992).

-fold higher gear ratio).

There also appears to be a minimum $\mathbf{V/V_{max}}$ at which fibers are used. For instance, if the white muscle does so well producing fast movements, why doesn't the fish have only one fiber type and let the white muscle power the slow swimming movements as well? The white muscle could certainly power slow swimming, but it is not used because its high $\mathbf{V_{max}}$ and 4-fold higher gear ratio would make its $\mathbf{V/V_{max}}$ at slow swimming speeds too low (i.e., 0.01-0.03, where the muscle is nearly isometric and efficiency is nearly 0; see shaded portion of Fig. 3e). At slightly faster swimming speeds, when the white muscle starts to be recruited to augment the power of the red, if the fish were to continue swimming steadily, the white muscle would still be shortening with too low a $\mathbf{V/V_{max}}$ to generate power efficiently. Under these circumstances, however, the fish employs "burst and coast swimming" in which it makes rapid tail beats (i.e., short duty cycle) with the white muscle to obtain a high V and to keep an optimal $\mathbf{V/V_{max}}$. At very slow swim speeds, (i.e., to the left of the shaded portion in Fig. 3d), carp also use the "burst and coast" pattern, but this time with the red muscle. This allows the fish's red muscle to make the normal SL excursion in less time (shorter duty cycle) resulting in normal $\mathbf{V/V_{max}}$ and efficiencies. Thus carp adopt a "burst and coast" pattern of swimming when the muscle fiber type being used would have too small a $\mathbf{V/V_{max}}$ to generate power with a high efficiency if the fish were swimming steadily (Rome et al. 1990a).

Thus given the constraints at both high $\mathbf{V/V_{max}}$ and at low $\mathbf{V/V_{max}}$, to achieve a full repertoire of movement, animals must use different fiber types with different $\mathbf{V_{max}}$'s and

different gear ratios. It should be further recognized that these "mechanical" constraints indirectly set the level of activity at which neuromuscular fatigue occurs. The white fibers have a low mitochondrial density and a low capillarity. Thus they have little ability to consume oxygen to replenish high energy phosphate stores. When swimming speed increases such that anaerobic fibers must be recruited to generate the requisite mechanical power (i.e., $\mathbf{V/V_{max}}$ of the red muscle becomes too high), the ATP used will be supplied anaerobically. This leads to white muscle lactate accumulation and glycogen depletion, and ultimately to fatigue. Therefore, swimming speeds at which anaerobic fibers are recruited are not sustainable (Rome et al. 1984). These mechanical constraints also explain the onset of neuromuscular fatigue at lower speeds at cold temperatures (see next section).

B. Different Muscle Temperatures in Carp

Raising the temperature of a muscle increases its $\mathbf{V_{max}}$. If $\mathbf{V/V_{max}}$ is an important design constraint, then the animal should use its muscle over a higher range of V's at the higher temperatures. Indeed, the $\mathbf{V_{max}}$ of carp red muscle is 1.6-fold greater at 20°C than at 10°C (Rome and Sosnicki, 1990). Although at a given swimming speed, the **V** at which the muscle shortens is independent of temperature, carp at 20°C could swim to 45 cm/s with the red muscle exclusively, while at 10°C they could only swim to 30 cm/s (Rome et al.1990a). Hence, the corresponding **V** at the respective maximum speed was 1.6-fold higher at 20°C than at 10°C (2.04 vs 1.28 ML/s respectively), resulting in the same $\mathbf{V/V_{max}}$ (0.36) at both temperatures. In addition, the 10°C fish could swim steadily at lower speeds than at 20°C, corresponding to a 1.6-fold lower **V** (resulting in the same $\mathbf{V/V_{max}}$ at the lowest speed). Thus at both 10 and 20°C, carp use their red muscle over the same range of $\mathbf{V/V_{max}}$ (0.17-0.36).

C. Fast swimming species (scup) vs slow species (carp)

At a given temperature, the marine scup can swim twice as fast with its red muscle as the fresh water carp (80 cm/s vs 45 cm/s at 20°C; Rome et al.1992a). We anticipated that the scup's maximum **V** (i.e., while swimming at 80 cm/s) would be twice as high as the carp's maximum **V** (i.e. while swimming at 45 cm/s). If maintaining $\mathbf{V/V_{max}}$ is important, then the $\mathbf{V_{max}}$ of scup should be twice as high as the carp's as well.

Remarkably, because scup employ a less undulatory style of swimming than carp (i.e. smaller backbone curvature and smaller SL excursion), at their respective maximum swimming speeds with red muscle, the **V**'s at which the muscles shorten are equal (about 2.04 ML/s; Rome et al.1992a). We now expected carp and scup red muscle should have the same $\mathbf{V_{max}}$, which is exactly what we found (Rome et al.1992b). Hence, both the fast fish and the slow fish use their red muscle over the same $\mathbf{V/V_{max}}$ (0.17-0.37) even though it corresponds to much higher swimming speed in scup.

D. Scaling of V_{max} with Body Mass (M_b) in Mammals

Although the muscles in mammals perform a variety of activities in addition to shortening (active lengthening and remaining isometric; Goslow et al.1981), $\mathbf{V/V_{max}}$ appears to be important in this muscle as well. Stride frequency at physiologically equivalent speeds scales with $M_b^{-0.16}$ (where M_b is body mass; Heglund and Taylor, 1988). As SL excursion may be independent of M_b, **V** should scale with $M_b^{-0.16}$ as well. Hence, the **V** in large animals should be much lower than in small ones, and thus to maintain a constant $\mathbf{V/V_{max}}$, the large animals should have a much lower $\mathbf{V_{max}}$. The $\mathbf{V_{max}}$ of large animals had never been previously measured largely for technical reasons. We developed single fiber histochemistry techniques and combined them with myosin light and heavy chain electrophoretic techniques to enable us to differentiate the 3 major fiber types (Sosnicki et al.1989). We then used single skinned fiber mechanics techniques, and measured $\mathbf{V_{max}}$ of three fiber types within the horse soleus muscle (Rome et al.1990b). The mean $\mathbf{V_{max}}$ varied over 10-fold between fiber types, which presumably provides the horse with the flexibility to power a wide range of motor activities.

By comparing $\mathbf{V_{max}}$ measured on the horse to that previously measured on the rat and on the rabbit, we examined scaling of $\mathbf{V_{max}}$ over a 1200-fold size range (Rome et al.1990b). The $\mathbf{V_{max}}$ of slow oxidative fibers (SO, Type I) scaled with $M_b^{-0.18}$ which is close to the $M_b^{-0.16}$ for stride frequency and **V**, suggesting that the SO fibers of large and small animals operate over the same $\mathbf{V/V_{max}}$ and at similar efficiencies. Fast glycolytic fibers (FG, Type IIb), on the other hand, scaled with $M_b^{-0.07}$, and thus FG fibers have a higher $\mathbf{V_{max}}$ in large animals than needed for maintaining a constant $\mathbf{V/V_{max}}$. FG fibers, however, are likely used infrequently, only when the horse is jumping or running at maximum speed. In this case the horse might be

willing to sacrifice efficiency for increased mechanical power provided by a higher V_{max}.

E. Summary of steady state design constraints

Thus, in four different cases which might lead to changes in V/V_{max}, evolution has taken the appropriate measures to maintain a constant V/V_{max}. In the three fish experiments, V/V_{max} is between 0.17 and 0.38, where power and efficiency are maximal (Fig. 1), showing that V/V_{max} is an important design constraint. The way animals produce a wide range of movements is by using fibers with different V_{max}'s and with different gear ratios. In the case of mammals, it appears that V_{max} scales appropriately to maintain a constant V/V_{max}, but it is not known precisely what this value is.

In conclusion, it appears that animals use their muscles over a narrow range of myofilament overlaps and over a narrow range of V/V_{max} where muscle generates maximum force and maximum power with optimal efficiency (Fig. 1). Therefore during evolution, three design parameters (gear ratio, V_{max} and myofilament lengths), appear to have been adjusted so as to obey these design constraints no matter what movement is made. Hence, these design constraints appear to be two of the rules by which muscular systems have been put together.

III. Non-steady state constraints

Although V/V_{max} and myofilament overlap appear to be important design constraints, they may not represent a complete description of muscle behavior during locomotion. The problem is that these constraints are based on the force-velocity and SL-tension curves, which are measures of steady state mechanics of maximally activated crossbridges. In this type of experiment, the muscle is stimulated at a fixed length (isometric) and is allowed to shorten only after generating maximum tension (indicating complete activation). The muscle is then given several minutes to relax (complete relaxation) prior to being relengthened and stimulated again. Although these steady state measurements are useful for studying the mechanics of contraction, this is not how the muscle is used during locomotion and thus may ignore other important constraints on muscle design. Unlike the steady state experiments, during cyclical locomotion muscle fibers alternately activate and relax and shorten and lengthen with no time delay in between (Josephson, 1985).

Intuitively it seems beneficial that fibers be fully "activated" during shortening and fully "relaxed" prior to relengthening. If the muscle were able to instantaneously activate and instantaneously relax then the mechanical behavior during shortening could be well described by steady state properties of muscle. Although during very low oscillation frequencies, muscle activation and relaxation requires a small fraction of the cycle and hence can be viewed as instantaneous, during oscillation frequencies that animals actually use during locomotion, the muscle may run into some important limitations.

Because the muscle cannot instantaneously relax (i.e., all the bridges detach so that subsequent lengthening of the muscle does not produce force), the muscle may have to operate in such a way that deactivation proceeds during shortening (Marsh, 1990). This could be achieved by cutting off the stimulus before the end of shortening and by an intrinsic property of the muscle called "shortening deactivation". If so, the crossbridges will not be maximally activated and force and power production will be below that described by the steady state force-velocity curve. In addition, incomplete relaxation would result in negative work. These competing effects are quantified by the net power during a complete cycle, which is equal to:

(work done by muscle $_{shortening}$ - work done on muscle $_{lengthening}$) per cycle x cycle freq.

From these considerations we anticipate that net power output during swimming may involve a complex interplay between different muscle properties. Thus, the effect of activation-relaxation kinetics on the mechanical behavior of muscle depends greatly on the conditions.

There is relatively little known about whether during locomotion the kinetics of activation and relaxation impinge on the mechanical performance of the muscle. The basic problem is that this can only be discerned by imposing the exact length changes and stimulation pattern the muscle undergoes in vivo on isolated muscle, and measuring force production. However, this has never been done before.

We have recently taken a first step toward this goal by imposing on isolated muscle in vivo length changes and oscillation frequencies and the in vivo stimulus duty cycle (measured from

EMGs). At 20°C, muscle bundles run under these in vivo conditions produced nearly maximal power, suggesting that the muscle works optimally during locomotion (Rome and Swank, 1992). This also suggests that the kinetics of activation and relaxation as well as crossbridge kinetics have been adjusted to produce maximum mechanical power at the oscillation frequencies and length changes that scup need to use during swimming. Further work using this approach will be useful in elucidating the design constraints of activation and relaxation.

Acknowledgments: This work was support by NIH grant AR38404

References

Gordon, A. M., Huxley, A. F. & Julian, F. J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibers. *Journal of Physiology* **184**, 170-192.

Goslow, G. E., Seeherman, H. J., Taylor, C. R., McCutchin, M. N. & Heglund, N. C. (1981). Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. *Journal of Experimental Biology* **94**, 15-42.

Heglund, N. C. & Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *Journal of Experimental Biology* **138**, 301-318.

Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society of London B* **126**, 136-195.

Josephson, R. K. (1985). Mechanical power output from striated muscle during cyclic contraction. *Journal of Experimental Biology* **114**, 493-512.

Lutz, G. & Rome, L. C. (1991). Design of frog muscle for jumping. *American Zoologist* **31(5)**, 123A.

Marsh, R. L. (1990). Deactivation rate and shortening velocity as determinants of contractile frequency. *American Journal of Physiology* **259**, R223-R230.

Rome, L. C., Loughna, P. T. & Goldspink, G. (1984). Muscle fiber recruitment as a function of swim speed and muscle temperature in carp. *American Journal of Physiology* **247**, R272-R279.

Rome, L. C., Funke, R. P., Alexander, R. M., Lutz, G., Aldridge, H. D., Scott, F. & Freadman, M. (1988). Why animals have different muscle fibre types. *Nature* **355**, 824-827.

Rome, L. C. (1990). The influence of temperature on muscle recruitment and function in vivo. *American Journal of Physiology* **259**, R210-R222.

Rome, L. C., Funke, R. P. & Alexander, R. M. (1990a). The influence of temperature on muscle velocity and sustained performance in swimming carp. *Journal of Experimental Biology* **154**, 163-178.

Rome, L. C., Sosnicki, A. A. & Goble, D. O. (1990b). Maximum velocity of shortening of three fibre types from the horse soleus: Implications for scaling with body size. *Journal of Physiology* **431**, 173-185.

Rome, L. C., Choi, I., Lutz, G. & Sosnicki, A. A. (1992a). The influence of temperature on muscle function in fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. *Journal of Experimental Biology* **163**, 259-279.

Rome, L. C., Sosnicki, A. A. & Choi, I. (1992b). The influence of temperature on muscle function in the fast swimming scup. II. The mechanics of red muscle. *Journal of Experimental Biology* **163**, 281-295.

Rome, L. C. & Sosnicki, A. A. (1990). The influence of temperature on mechanics of red muscle in carp. *Journal of Physiology* **427**, 151-169.

Rome, L. C. & Sosnicki, A. A. (1991). Myofilament overlap in swimming carp. II. Sarcomere length changes during swimming. *American Journal of Physiology* **260**, C289-C296.

Rome, L. C. & Swank, D. (1992). The influence of temperature on power output of scup red muscle during cyclical length changes. *Journal of Experimental Biology* **Submitted.**

Sosnicki, A. A., Lutz, G. J., Rome, L. C. & Goble, D. O. (1989). Histochemical and molecular identification of fiber types in single, chemically skinned equine muscle cells. *Journal of Histochemistry and Cytochemistry* **37**, 1731-1738.

Sosnicki, A. A., Loesser, K. & Rome, L. C. (1991). Myofilament overlap in swimming carp. I. Myofilament lengths of red and white muscle. *American Journal of Physiology* **260**, C283-C288.