

DYNAMICS OF MUSCLE FUNCTION DURING LOCOMOTION: ACCOMMODATING VARIABLE CONDITIONS

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Accepted 9 June; published on WWW 16 November 1999

Summary

Much of what we know about animal locomotion is derived from studies examining animals moving within a single, homogeneous environment, at a steady speed and along a flat grade. As a result, the issue of how musculoskeletal function might shift to accommodate variability within the external environment has remained relatively unexplored. One possibility is that locomotor muscles are differentially recruited depending upon the environment in which the animal is moving. A second possibility is that the same muscles are recruited, but that they are activated in a different manner so that their contractile function differs according to environment. Finally, it is also possible that, in some cases, animals may not need to alter their musculoskeletal function to move under different external conditions. In this case, however, the mechanical behavior appropriate for one environmental condition may constrain locomotor performance in another. To begin to explore the means by which animals accommodate variable conditions in their environment, we present three case studies examining how musculoskeletal systems function to allow locomotion under variable conditions: (1) eels undulating through water and across land, (2) turkeys running on level and inclined surfaces, and (3) ducks using their limbs to walk

and to paddle. In all three of these examples, the mechanical behavior of some muscle(s) involved in locomotion are altered, although to different degrees and in different ways. In the running turkeys, the mechanical function of a major ankle extensor muscle shifts from contracting isometrically on a flat surface (producing little work and power), to shortening actively during contraction on an uphill gradient (increasing the amount of work and power generated). In the ducks, the major ankle extensor undergoes the same general pattern of activation and shortening in water and on land, except that the absolute levels of muscle stress and strain and work output are greater during terrestrial locomotion. In eels, a transition to land elicits changes in electromyographic duty cycles and the relative timing of muscle activation, suggesting some alteration in the functional mechanics of the underlying musculature. Only by studying muscle function in animals moving under more variable conditions can we begin to characterize the functional breadth of the vertebrate musculoskeletal system and understand more fully its evolutionary design.

Key words: dynamics, muscle function, locomotion, variability.

Introduction

Muscles function to counterbalance loads and to control the movements of animals over a range of dynamic conditions. These conditions can be expected to vary when animals change gait or alter speed or when physical aspects of the external environment change. Classical studies, however, have traditionally examined the properties of muscles under quasi-static rather than dynamic conditions (McMahon, 1984). Such studies have provided important insights into the force-velocity (Hill, 1938) and force-length (Gordon et al., 1966) relationships of muscles that have proved fundamental to our understanding of how muscles work. However, because of the time-varying nature of muscle activation, force development and length change during actual locomotor movements, it is essential that the contractile behavior of

muscles also be studied under *in vivo* conditions. New methods allow direct recordings of changes in muscle force and length in naturally behaving animals and, thus, provide the opportunity to re-examine the properties of muscles under more dynamic conditions.

On a volume-specific basis, vertebrate striated muscles have broadly similar capacities to perform mechanical work. However, the functional role of a muscle is strongly influenced by its architecture as well as by its biochemical properties. Pennate muscles with shorter fibers contract over more limited ranges of length but typically have a greater fiber cross-sectional area, which enables them to generate greater forces. In contrast, parallel-organized muscles with longer fibers can shorten over a greater length with a higher velocity, but tend

to produce lower levels of force because of their smaller cross-sectional area. Thus, a basic trade-off exists between a muscle's ability to shorten actively and to generate mechanical power (work per unit time) *versus* its ability to contract nearly isometrically and to generate force economically (reducing the amount of ATP consumed per force generated). In general, longer-fibered muscles with faster-contracting myosin have the capacity to generate greater power than shorter-fibered muscles with slower-contracting myosin. However, shorter-fibered muscles require fewer cross-bridges to generate a given amount of force, lowering their cost of force generation. Given their limited capacity to change length, short-fibered muscles may be expected to generate force under nearly isometric conditions. By contracting isometrically, or with a brief initial period of active stretch, muscles can lower the energy cost further because of their ability to generate considerably larger forces compared with when they shorten (Fig. 1). This derives directly from the force-velocity relationship and allows the recruitment of fewer fibers (motor units) per unit force generated. Short-fibered muscles also often transmit force *via* long tendons, which provide elastic energy savings that may further reduce metabolic cost.

Shorter-fibered muscles that attach to longer tendons, however, are limited in their ability to control length changes that result from tendon stretch (Ker et al., 1988; Rack and Ross, 1984). This effect is most extreme in many of the leg muscles of ungulates, which can have tendons that can be 40–50 times the length of the muscle's fibers (Bertram and Marsh, 1998; Biewener, 1998; Dimery et al., 1986). Consequently, these muscles have little ability to compensate for stretch of their tendons and, hence, to control distal limb position. Other longer-fibered muscles presumably must be recruited to control limb position. Position control therefore favors longer-fibered muscles with little or no tendon and, thus, probably represents an important trade-off in the capacity of muscles to generate force.

These architectural features of muscles and tendons suggest constraints on function. Certain muscles, such as those in the limbs of ungulates and hopping macropods, may be well suited for energy economy and tendon elastic storage. Others, such as those in the legs of frogs or the flight musculature of birds, may be better suited for contracting over greater lengths and for generating mechanical power (Fig. 1). When an animal moves at steady speeds, its muscles may be expected to contract under fairly uniform conditions (from one stride to the next). However, when an animal changes gait, accelerates or runs up an incline, the contractile function of some of its muscles probably must change. A potentially more extreme case of altered motor function arises when an animal must make a transition between locomotor environments, as when shifting between aquatic and terrestrial locomotion. How do the musculoskeletal systems of animals accomplish these tasks?

Changes in motor function can be met either by a change in the contractile behavior of individual muscles or *via* an alteration in the recruitment pattern of muscles within the limbs and body (or both). If muscle-tendon architecture imposes a

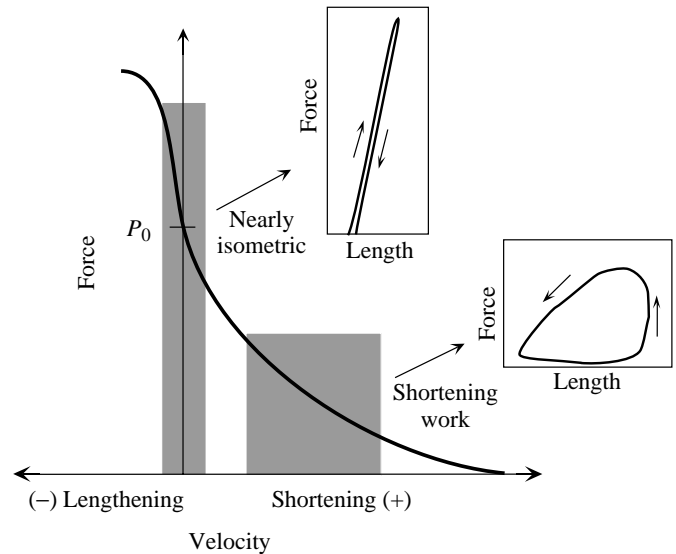


Fig. 1. Schematic representation of the force-velocity curve for striated skeletal muscle depicting the range of force and velocity over which muscles that generate force isometrically (P_0 is the isometric force), or with a brief initial stretch, operate compared with muscles that shorten to perform work and generate mechanical power. Insets to the right show the corresponding force-length behavior ('work loop') of a muscle under both these conditions. The area contained within the force-length loop is the net work produced (or absorbed, if in a clockwise direction) by the muscle. The counterclockwise work loop for muscles that generate mechanical power indicates positive work, whereas muscles that contract nearly isometrically generate or absorb very little work. Leg muscles of animals that use bouncing gaits (e.g. running and hopping), therefore, may be expected to operate nearly isometrically, while muscles that power swimming, flying and jumping may be expected to shorten considerably to perform work.

functional constraint on certain muscles, this would suggest that a change in the pattern of muscle recruitment is required to enable broad changes in motor function. In contrast, use of the limb may be anatomically constrained by the need to utilize the same muscle, or set of muscles, despite differing locomotor conditions. In this case, locomotor capacity under one or both conditions might be limited. In this paper, three examples of variation in locomotor function are examined that provide instances in which these functional trade-offs between locomotor capacity and musculoskeletal design are likely to be important.

Aquatic versus terrestrial undulations: axial muscle function in eels

Anguillid eels are elongate fish that are well known for their abilities to locomote across land as well as through water (Gray, 1968; Lindsey, 1978; Tesch, 1977). In both environments, nearly all the forces responsible for generating forward thrust are derived from the axial, rather than the appendicular, musculoskeletal system. An eel's axial muscle

can be divided into a thin, superficial band of red, oxidative fibers, which are generally oriented parallel to the long axis of the fish, and a deeper, serially arranged set of myomeres, each consisting of white, glycolytic fibers organized in a complex manner (Alexander, 1969). This musculoskeletal design is, in general, similar to that of other fishes and has presumably evolved to produce effective propulsive thrust through water. By quantifying the patterns of movement and underlying muscle activity associated with both aquatic and terrestrial undulatory locomotion in eels, we can begin to understand how this musculoskeletal system, which is designed for propulsion in one environment, is also able to produce locomotion in another, quite different, physical environment.

White myomeric muscle was implanted with fine-wire bipolar electrodes at a variety of positions along the body of anesthetized eels (35–42 cm total length, L) to characterize variations in the timing and magnitude of electromyograms (EMGs) from axial muscle during locomotion in different environments. Once the animals had recovered from anesthesia, they were videotaped (250 frames s^{-1}) either swimming across a range of speeds (0.5–1.0 Ls^{-1}) within a flow tank (28 cm × 28 cm × 78 cm working section) or undulating across wet packed sand (0.2–0.6 Ls^{-1}) within a plastic enclosure (1.3 m diameter). Analog EMG signals were amplified, filtered and converted to digital signals, which were then analyzed using a personal computer. High-speed video recordings were used to determine the temporal patterns of displacement and flexion of intervertebral joints along the bodies of undulating eels. Using X-rays of animals after the experiments, the longitudinal positions of all electrode implants were determined. The patterns of intervertebral flexion at the joints spanned by muscle fibers from which EMG activity was recorded were then quantified using a custom-designed kinematic analysis program described by Jayne and Lauder (1993) and Gillis (1997). As the high-speed video recordings were synchronized with the EMG signals, the timing of muscle activity could be related to the *in vivo* patterns of muscle strain indirectly estimated from the patterns of intervertebral flexion. Thus, the magnitude and duration of EMG bursts as well as their timing relative to the sinusoidal lengthening and shortening of axial muscles could be compared between aquatic and terrestrial locomotion. For more details of the methods described above, see Gillis (1998b; G. B. Gillis, manuscript submitted).

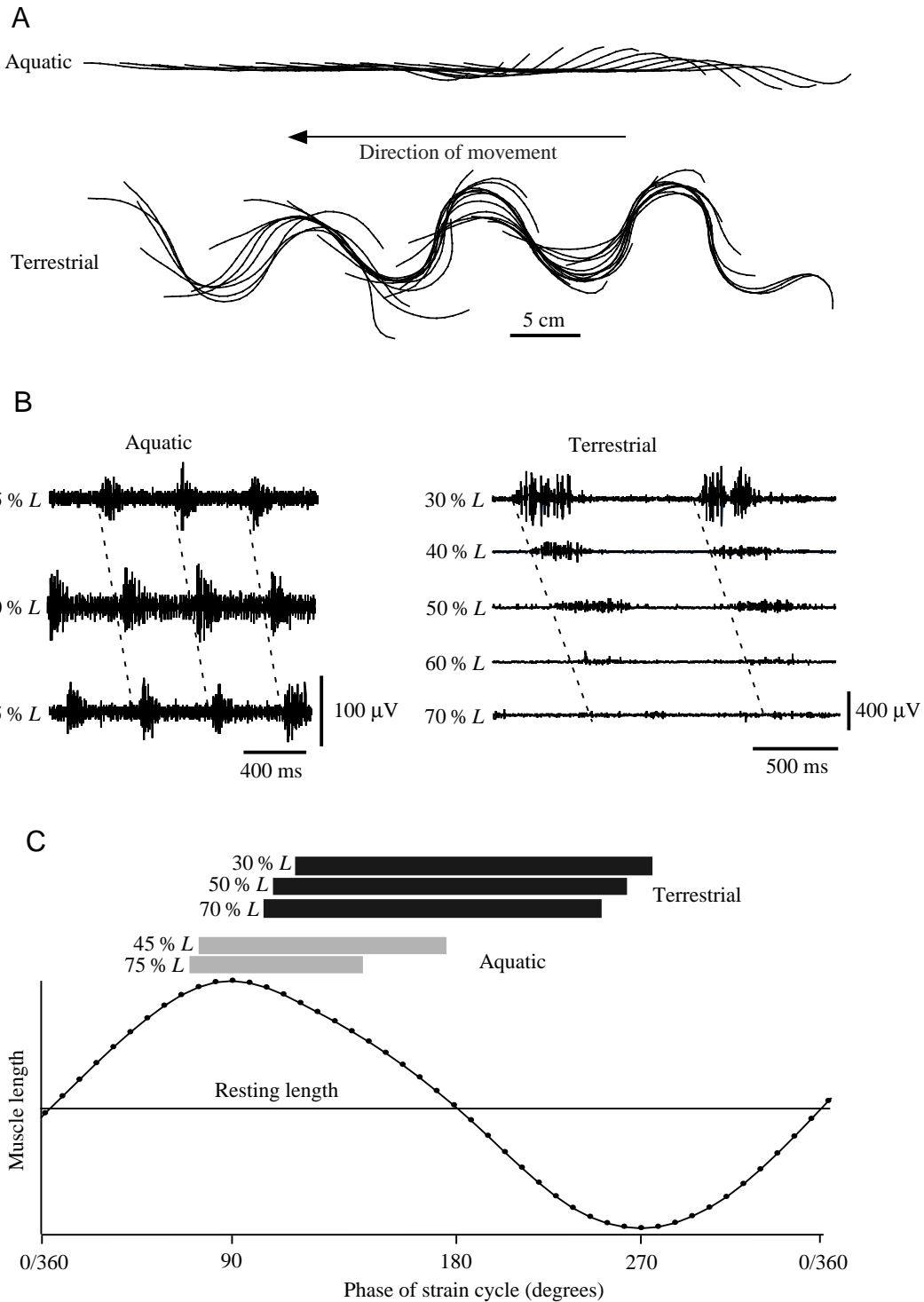
Locomotor kinematics change drastically when an eel undulates across a terrestrial surface relative to when it is swimming (Fig. 2A). On land, undulatory amplitude and intervertebral flexion are greater along the entire body than during swimming. In addition, on land, the entire body is bent into high-amplitude waves. In the water, the tail undergoes much higher amplitude undulations than does the head, which only begins to undulate noticeably at high swimming speeds or during accelerating movements. Finally, on land, most parts of the body follow the same general path of travel, whereas in water the tail follows a very different path (with high-amplitude undulations) from the head (Gillis, 1998a).

Underlying these kinematic differences between aquatic and terrestrial locomotion are clear changes in the muscle activity patterns underlying locomotion. Although, in both environments, eels pass alternating waves of muscle activity from anterior to posterior (Fig. 2B), closer examination of the duration, intensity and timing of the EMG bursts making up these waves reveals fundamental changes.

The absolute duration of EMG bursts is much greater at all body positions during terrestrial locomotion than during swimming (Fig. 2B,C). However, it is important to keep in mind that EMG burst durations (in absolute time) are directly related to undulatory cycle time (the time required for any part of the body to go through one cycle of undulation) and inversely related to locomotor speed. Eels typically move much more slowly across land (maximum speeds observed here are approximately 0.6 Ls^{-1}) than through water (maximum speeds observed are greater than 2.0 Ls^{-1}), with undulatory cycle durations on land typically being greater than those observed during swimming. Hence, it is not particularly surprising that absolute EMG burst durations are greater during terrestrial locomotion. Nonetheless, one can quantify EMG burst duration relative to the undulatory cycle time (i.e. EMG duty cycle), which in undulating fish does not vary with locomotor speed. Such calculations reveal that EMG duty cycles are significantly longer (0.4–0.5 cycles for white muscle) during terrestrial locomotion than during swimming (0.2–0.3 cycles for white muscle, 0.3–0.4 cycles for red muscle) (Fig. 2C). Therefore, the relative period of electrical activation in axial muscles is being altered so that muscles are stimulated for greater proportions of each undulatory cycle on land.

In addition to longer-duration periods of muscle activity, eels also use bursts of significantly greater intensity (rectified area of the EMG burst/absolute burst duration) when on land (Fig. 2B). Although comparisons of EMG intensities across different electrode implants and animals must be treated with caution, the consistency and magnitude of the differences found between environments using identical electrode design strongly suggest that real increases in the intensity of axial muscle activity are required to move on land relative to when the same animal moves at the same speed in the water. The increase in the intensity (and probably the duration) of EMG signals during terrestrial locomotion is probably a means of augmenting force production to counteract the gravitational forces and additional load-bearing required for moving on land. For example, similar shifts in muscle activity patterns are seen in crustaceans bearing increased loads as the result of a shift from water to land, limb amputation or artificial placement of weights on the body (Clarac et al., 1987; Grote, 1981).

Furthermore, the relative timing of EMG activity during an undulatory cycle also depends upon the nature of the external environment. During swimming, as axial muscle fibers cyclically lengthen and shorten as the body repeatedly bends, electrical activation of the axial musculature anywhere along the body always begins late in the lengthening phase of that muscle's strain cycle, prior to muscle shortening (Fig. 2C).



This is a pattern typical of muscles operating under such conditions, whether they be in the axial musculature of another species of fish (e.g. Wardle et al., 1995), a swimming salamander (Frolich and Biewener, 1992) or in the flight muscle of a flying bird (Dial, 1992). This pattern is thought to maximize work output from the muscle (Josephson, 1993). However, during terrestrial undulations, although the muscle fibers still undergo sinusoidal cycles of lengthening and

shortening (of higher amplitude), their period of activation shifts to later in the strain cycle. This results in the onset of EMG activity at any point along the body occurring after shortening has already begun. This shift in the timing of EMG bursts is likely to have an effect on the mechanical function of the muscle although, without direct *in vivo* or *in vitro* analyses of fiber length change and force production, the effect of this shift in stimulation phase will remain speculative.

Fig. 2. Kinematics, electromyograms (EMGs) and the timing of muscle activity relative to estimated muscle strain during aquatic and terrestrial locomotion in the eel. (A) Two series of eel midlines reconstructed from high-speed video sequences of the same animal moving at the same average speed ($0.4Ls^{-1}$, where L is total body length) in water and on land. On land, waves of undulation can be seen along the entire body, and undulatory amplitude at all sites is quite high. In contrast, in water, it is only the more posterior regions of the animal that undergo obvious undulations, and amplitude is therefore very low anteriorly, increasing to moderately high levels posteriorly. (B) Traces of filtered EMG recordings from axial muscle at different positions during both swimming and terrestrial locomotion. Recordings from swimming eels are from red muscle, since white muscle is only recruited along large portions of the body at very high speeds or during unsteady behaviors. Terrestrial recordings are taken from white muscle, since electrodes in red muscle were often pulled out because of their shallow level of implantation and the exaggerated axial movements on land. In both environments, muscle activity along the length of the body in a wave-like fashion (i.e. more-anterior sites are activated earlier than more-posterior sites on the same side, as revealed by the diagonal broken lines connecting EMG burst onsets). However, EMG burst intensity at any site is on average much greater on land than during swimming (although in the tail, burst intensities on land decrease dramatically). (C) Bar diagram showing the duration and timing of white muscle EMG activity at different positions relative to site-specific muscle strain in both environments. Dark bars represent activity on land, while lighter bars show activity during swimming. EMG duty cycle (burst duration/cycle duration) is significantly longer during undulatory locomotion on land, and the timing of muscle activity is also much later in the strain cycle. Such differences in the temporal aspects of muscle activity, combined with differences in EMG intensity, suggest differences in the mechanical behavior of muscle fibers across environments.

A hypothetical explanation for this unusual pattern of stimulation relative to muscle length change (i.e. a muscle shortening, or beginning to shorten, without active contraction) relates to the fact that the path of movement of most parts of the animal on the sandy substratum is constrained to the path traced by the anteriormost regions of the eel. This is because the weight of the animal creates a groove in the sand, through which the rest of the body then typically moves. As any part of the animal moves through a curved portion of this groove, the vertebrae in that body segment will flex to accommodate the curve in the path, and muscles spanning those joints will accordingly change length. If muscles in regions of the body beyond the curve are generating the forces responsible for pushing or pulling the portion of the body within the curve through it, then muscle fibers in that region will have changed length passively simply as a result of having to bend and stretch to accommodate the movement through the curve. A more detailed explanation of this phenomenon can be found in G. B. Gillis (manuscript submitted).

Finally, it should be noted that, during terrestrial undulatory locomotion, white myomeric muscle is recruited along most of the body to move at any speed. During swimming, it is largely red muscle that is used for steady swimming, while white

muscle is only recruited at the highest swimming speeds or during acceleratory or escape behaviors. This might at first appear to exemplify a discrete shift in muscle recruitment related to a shift in the external environment. However, differential fiber-type recruitment (similar to differential EMG burst intensity) is likely to be tightly linked to locomotor effort. Axial muscles must increase their force and work production during terrestrial locomotion to counteract the increased gravitational load associated with moving onto land. However, eels must also increase their effort to increase swimming speed (to overcome the exponentially increasing levels of drag associated with faster swimming speeds) and, accordingly, show increases in burst intensity and in white muscle recruitment when doing so. It happens to be the case that higher levels of effort are required to move at a given speed on land relative to the same speed in water, but aquatic behaviors exist that can elicit similar directional shifts in burst intensity and fiber-type recruitment. Therefore, we suggest that differences in burst intensity and fiber-type recruitment are not directly related to an environmental shift *per se* but to differences in effort across environments that are required to move at similar speeds. It is really the changes in duty cycle and timing that do not ever appear to be approached during aquatic behaviors that represent the functional shift in the axial musculoskeletal system of eels to accommodate drastic shifts in the external environment.

In conclusion, eels accommodate a gross transition in the external environment by altering the underlying motor patterns driving the locomotor movements. Shifts in both the EMG duty cycle and in the overall timing of muscle activation relative to muscle strain accompany a transition into the terrestrial environment. And it is these differences in the relative duration and timing of activity that suggest that the mechanical behavior of these muscles probably differs across environments. Nevertheless, there also appear to be trade-offs in locomotor performance related to using the same muscles for swimming and moving on land. For example, eels cannot move nearly as fast across a terrestrial surface as they can through water. It is also likely that eels cannot move on land as fast or as economically as snakes, whose axial musculoskeletal design is quite different from that of fish and has been derived from a terrestrial ancestor.

Level versus incline locomotion

Terrestrial running and hopping gaits involve oscillatory movements of the body's center of mass, during which the body's kinetic and potential energy can be converted into elastic strain energy that is stored and recovered from tendons and ligaments during the support phase of the stride (Alexander, 1984; Cavagna et al., 1977). A simple mass-spring system represents well the basic movements of the animal for these gaits, in which the body essentially bounces on a spring-like limb (Blickhan, 1989; Farley et al., 1993; McMahon and Cheng, 1990). It has been argued that the function of key limb muscles under conditions of steady level locomotion using

these gaits is mainly one of economical force generation with minimal length change (Roberts et al., 1997; Taylor, 1994), rather than the production of mechanical work. What evidence is there that some limb muscles of terrestrial animals contract isometrically during limb support?

One indirect piece of evidence is that the energy cost of terrestrial locomotion in birds and mammals as a function of size and speed can be explained largely by the magnitude and rate of force generated by muscles to support an animal's weight (Kram and Taylor, 1990). It is not explained by the amount of work performed by muscles to move the body (Heglund et al., 1982). Because the muscles of larger animals exert smaller mass-specific forces (Biewener, 1989), but do so with longer fibers, the relative volume of muscle that is activated for equivalent levels of performance is generally equivalent in different-sized animals. As a result, the rate of force development (quantified by Kram and Taylor as the inverse of limb contact time, $1/t_c$) appears to explain most of the variation in cost with speed and size. Additional evidence comes from direct recordings of muscle force (*via* a strain gauge attached to the calcified tendon) and length change (*via* sonomicrometry) in the lateral gastrocnemius muscle of running turkeys (*Meleagris gallapavo*; Roberts et al., 1997). These measurements show that the lateral gastrocnemius generates force with only small changes in length (6% of resting length; Fig. 3A) when the turkeys run on a level surface. Similar recordings obtained from the lateral gastrocnemius and plantaris muscles of wallabies (*Macropus eugenii*) hopping on a level surface (Biewener et al., 1998) demonstrate that key leg muscles of these animals also generate force with little length change (in this case, less than 2–6% of resting length). In wallabies, the amount of elastic energy recovered from the muscles' tendons exceed by 30-fold the amount of work performed by the muscles.

With a shift from level to incline locomotion, limb muscles must perform additional work equivalent to the potential energy gained by the animal's body during each step. In the case of turkeys (Roberts et al., 1997), incline running results in an increase in the amount of shortening by the lateral gastrocnemius to increase the amount of work that it performs (Fig. 3B). In this case, the contractile behavior of an individual muscle is altered to facilitate the amount of mechanical work performed. For muscles with more extreme architectural specialization for economical force development and tendon elastic energy storage, however, the ability to shift from isometric to positive work output may be more constrained. This would be expected for the highly specialized distal leg muscles of many ungulates, in which the muscle's volume is so small, and the fibers are so short, that there is almost no capacity to do work (Bertram and Marsh, 1998; Biewener, 1998; Dimery et al., 1986). Given such a constraint, it seems likely that incline locomotion would require a shift in motor recruitment among muscles of the limb, so that other muscle groups (hip or knee extensors) shorten more to increase their work output in order to meet the required increase in potential energy gain. Future studies of level *versus* incline locomotion

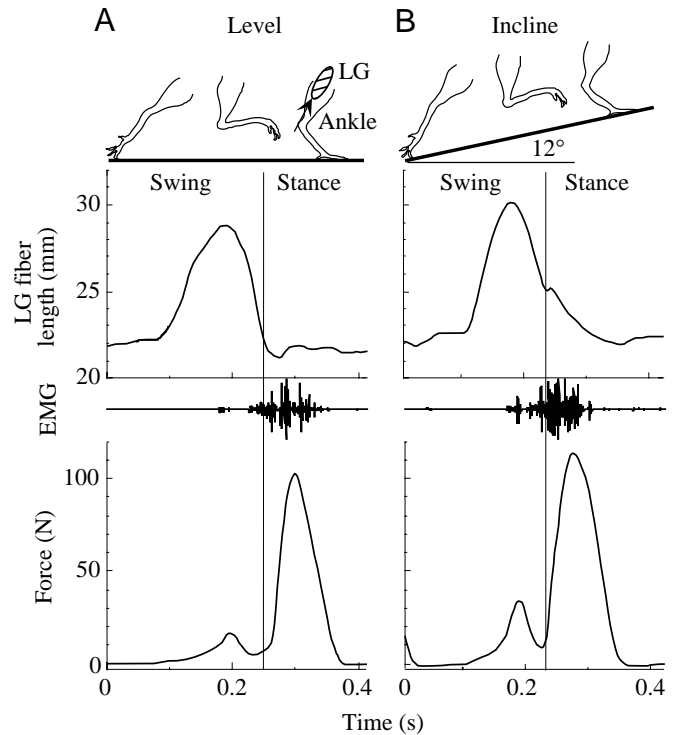


Fig. 3. *In vivo* force, electromyogram (EMG) and length recordings obtained from the lateral gastrocnemius of a turkey running (A) on the level and (B) up an incline (modified from Roberts et al., 1997). Whereas the lateral gastrocnemius changes length considerably during the swing phase of the stride, it shortens by only 6% of its resting length during the support phase of level running. This is the time during which force is actively generated by the muscle. When running up an incline, the muscle is stretched to a greater length and begins to develop force as it continues to shorten. As a result, the muscle shortens over a greater range during active force generation, allowing it to do more work (30-fold increase) and helping to increase the potential energy of the animal as it moves up the incline. LG, lateral gastrocnemius muscle.

are needed to examine the relative importance of shifts in recruitment pattern *versus* shifts in the contractile behavior of individual muscles in allowing terrestrial animals to cope with non-level terrain in their natural environments.

Aquatic *versus* terrestrial gait: leg muscle function in ducks

Dabbling ducks, such as mallards (*Anas platyrhynchos*), swim at the surface of the water and locomote on land. Consequently, their hindlimbs must provide an effective means of fluid propulsion during swimming as well as weight support and thrust production during walking and running. The gastrocnemius muscle is key to both of these functions. By comparing its mechanical function during these activities, we examine the capacity of the gastrocnemius to perform mechanical work during swimming *versus* economical force generation during walking and running. In doing so, we ask whether this muscle is capable of shifting its contractile

function to accomplish these tasks or whether it is constrained to operate in a more limited fashion.

The medial and lateral heads of the mallard gastrocnemius attach *via* separate tendons before forming a common Achilles tendon. This allows us to compare isolated force recordings of the lateral gastrocnemius of one limb with forces transmitted by the common tendon of the whole muscle of the opposite limb using tendon buckle force transducers (for details, see Biewener and Baudinette, 1995). We use these recordings to evaluate the agonist recruitment of the medial and lateral heads for alternating locomotor cycles. In addition to the tendon force transducers, sonomicrometry (Sonometrics, 0.7 mm crystals) and EMG electrodes were implanted mid-belly in the lateral gastrocnemius parallel to the fiber axis of the muscle (which is bipennate).

During swimming, oscillatory length changes of the lateral gastrocnemius are fairly symmetrical with respect to shortening and lengthening (Fig. 4A). Force development by the lateral gastrocnemius occurs during the time when the muscle shortens and is near zero while the muscle lengthens. Forces generated by the lateral gastrocnemius average $66 \pm 15\%$ (mean \pm s.d., $N=103$) of the total force transmitted by both the medial gastrocnemius and lateral gastrocnemius together. Because the lateral gastrocnemius is the larger of the two muscles (lateral gastrocnemius fiber area averages 1.39 times medial gastrocnemius fiber area), peak stresses developed in the lateral gastrocnemius are 36 ± 9 kPa compared with 26 ± 8 kPa ($N=103$) in the medial gastrocnemius. Although the sonomicrometry recordings show that the muscle shortened over the entire time that it developed force, measurements of ankle flexion early in the propulsive stroke suggest initial lengthening of the muscle and tendon, before subsequent shortening to extend the ankle. Thus, tendon stretch, facilitated by the low stiffness of the tendon at low force levels (Bennett et al., 1986; Shadwick, 1990), must account for all of the length increase indicated by ankle flexion in addition to the amount due to fiber shortening.

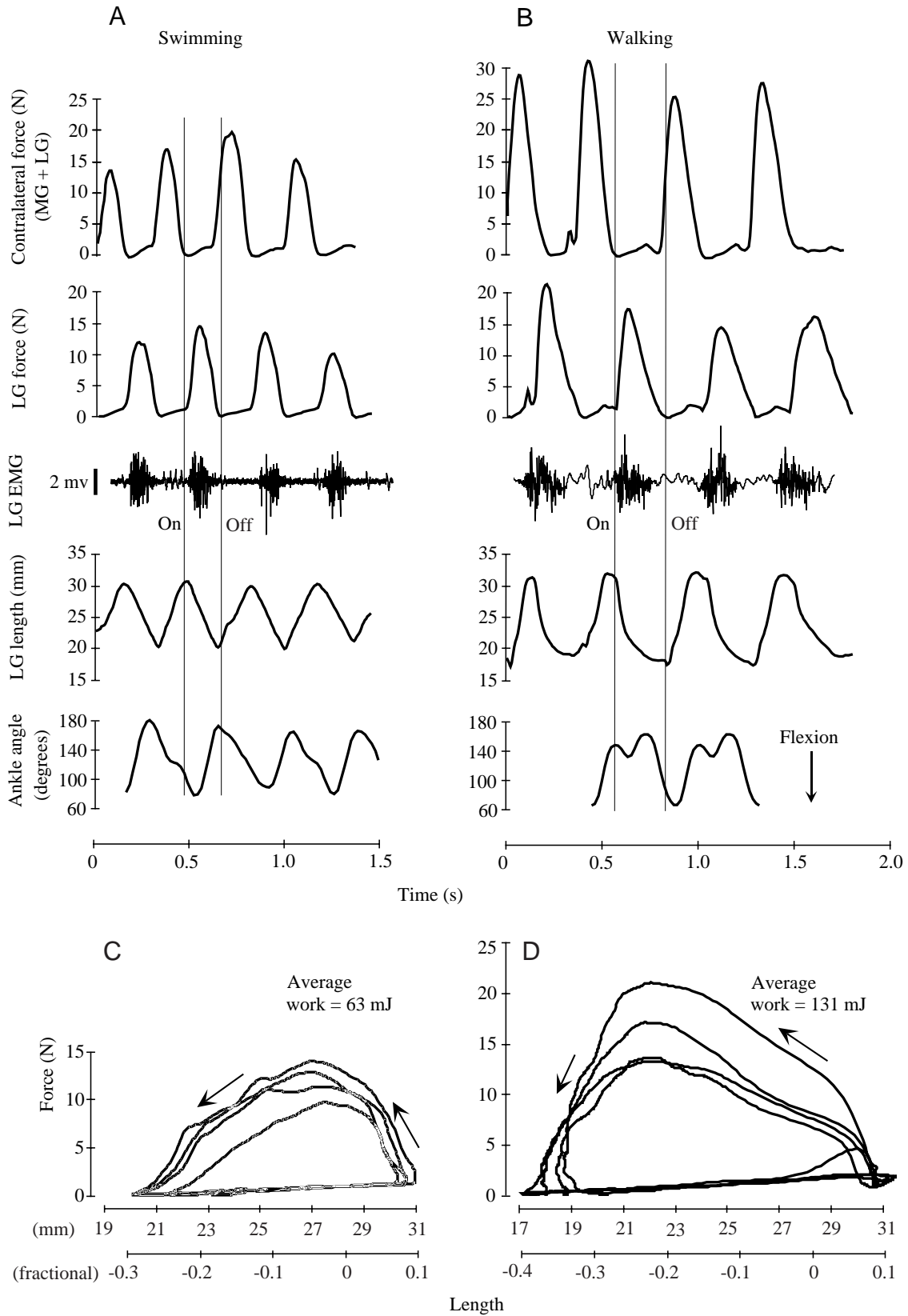
During walking and running, length changes of the lateral gastrocnemius are more irregular in the pattern of lengthening and shortening within a cycle compared with swimming (Fig. 4B). Whereas the muscle is rapidly lengthened during the swing phase, the muscle shortens at a progressively decreasing rate throughout the support phase. As is the case during swimming, the lateral gastrocnemius develops force while it shortens and force is near zero while the muscle is being lengthened. Forces generated by the lateral gastrocnemius during walking and running average $59 \pm 22\%$ ($N=84$) of the total force transmitted by both the medial gastrocnemius and lateral gastrocnemius together, matching fairly closely the difference in size between the two muscles. In contrast to swimming, therefore, peak stresses developed in the two muscle agonists during terrestrial locomotion are similar: 64 ± 11 kPa in the lateral gastrocnemius compared with 61 ± 14 kPa ($N=84$) in the medial gastrocnemius. During terrestrial locomotion, ankle flexion at the beginning of the support phase is followed by a brief period of extension and

subsequently by a more prolonged period of flexion. Consequently, although ankle joint kinematics again suggest lengthening of the muscle and its tendon at the beginning of force development early in support, the sonomicrometry recordings show that all the lengthening occurred by stretch of the tendon and not of the muscle's fibers.

An important observation emerging from direct measurements of length change by means of sonomicrometry, such as these, is that muscles may not undergo a period of active stretch early in the support, or propulsive, phase. Traditional interpretations of muscle length change based on joint kinematics often suggest that extensor muscles are stretched early in limb support during joint flexion (during the 'yield' E2 phase of the stride; Goslow et al., 1973; Philippson, 1905; Walmsley et al., 1978). However, our present data, as well as those obtained using similar recording methods for the medial gastrocnemius of walking cats (Griffiths, 1991) and the lateral gastrocnemius of hopping wallabies (Biewener et al., 1998), demonstrate that muscle fibers may shorten against the series elastic stretch of the tendon, particularly at low force levels when the tendon is most compliant. As a result, all the length increase indicated by joint flexion may occur in the tendon alone. Importantly, the absence of muscle fiber stretch calls into question traditional interpretations of spindle stretch receptor activation to enhance motor drive to the muscle *via* Ia afferents to the motor neuron pool of the muscle (Houk, 1979; Prochazka, 1986).

When force is plotted *versus* length change, the counterclockwise *in vivo* work loops produced by the lateral gastrocnemius of mallards during swimming are fundamentally similar to those produced during walking and running (Fig. 4C,D). For both modes of locomotion, the muscle performs substantial positive work during each locomotor cycle. The greater work achieved during terrestrial locomotion is a product of both greater shortening and greater force. In both locomotor modes, however, the amount of muscle shortening is considerable. During swimming, the lateral gastrocnemius shortens by a total of 24% of its resting length, and during walking and running it shortens by 35–40% of its resting length. Because the muscle is nearly fully relaxed as it is being lengthened, it does little or no negative work during the swing or protraction phase of the locomotor cycle.

The broad counterclockwise work loops of the lateral gastrocnemius indicate fundamentally similar contractile behavior during both swimming and terrestrial gaits. In contrast to the lateral gastrocnemius of running turkeys (Fig. 3, modified from Roberts et al., 1997) or the lateral gastrocnemius and plantaris of hopping wallabies (Biewener et al., 1998), there is no evidence of the isometric, or stretch-activated, force development characteristic of contractile behavior that would enhance economical force generation. To a certain extent, the uniform behavior of the lateral gastrocnemius may reflect the fairly limited range of speeds that we observed for the mallards during terrestrial gaits (0.3 – 1.7 m s⁻¹), in which the majority of trials were walks. Although this may reflect a limited locomotor capacity of mallards on land, recordings obtained at



faster speeds known to be a running gait are needed to confirm whether the contractile behavior of the lateral gastrocnemius is limited to the extent observed here. Similarly, it would be

informative to study the contractile function of turkey (or other galliform) leg muscles during walking in comparison with running to determine whether a pattern of isometric behavior

Fig. 4. *In vivo* force, electromyogram (EMG) and length recordings obtained from the lateral gastrocnemius of a mallard during (A) swimming (0.35 m s^{-1}) and (B) walking (0.6 m s^{-1}), for which cycle frequency is approximately equal. These are compared with combined force recordings obtained from the medial (MG) and lateral (LG) gastrocnemius muscles of the contralateral limb. Light vertical lines indicate the support phase of the limb corresponding to the isolated LG force, EMG and length recordings. Angular changes of the ankle joint of this limb are also shown. Work loops obtained from the force-length behavior of the lateral gastrocnemius for the same series of cycles are shown for swimming (C) and for walking (D). In both cases, the work loops are counterclockwise in direction, indicating that positive work is produced during each cycle (mean values are indicated).

is maintained or changes with changes in gait. Nevertheless, it seems likely that, together with other morphological features adaptive to swimming, such as webbed feet and a broad pelvis, the functional need of the mallard lateral gastrocnemius to generate positive power during swimming may restrict its ability to generate force with limited length change and reduced energy expenditure during terrestrial gaits. In this particular example, the potential for a substantial shift in muscle function associated with a change in locomotor mode is not observed. Instead, the mallard's terrestrial locomotor capacity appears to be constrained by the importance of its swimming ability, which requires a trade-off in muscle properties.

Conclusion

Many animals move through complex and heterogeneous physical environments at varying speeds and using different modes of locomotion. Yet much of what we know about how muscles operate to drive these locomotor movements comes from studies examining animals or muscles moving at a constant velocity (or across a narrow range of velocities) and often within a single, homogeneous environment. To begin to address issues relating to variability in motor function, we have provided three examples of how musculoskeletal systems act to accommodate gross changes in the external environment. We set forth two hypotheses (not mutually exclusive) as to how such accommodation might be made. First, patterns of recruitment might be altered. In this case, it would be expected that certain muscles within the limbs or bodies of animals are architecturally designed to perform under rather specific conditions and that, if other conditions are encountered, different muscles will need to be recruited. Alternatively, the same muscles might be recruited under different conditions, suggesting either that locomotor performance will be constrained in certain conditions or that the mechanical behavior of such muscles can be changed *via* alterations in the patterns of muscle stimulation and strain. Finally, a combination of these two strategies might be utilized.

In all three examples presented here, similar muscles seem to be recruited to accommodate either an aquatic-to-terrestrial transition or a shift in the angle of the terrestrial surface. In

mallard ducks, it would appear that the mechanical behavior of the major ankle extensor functions similarly in both water and on land, but that this then constrains the locomotor performance of the animal when it moves on land. In contrast, turkeys appear to shift the mechanical function of their major ankle extensor when running uphill (when the gastrocnemius actively shortens and generates significant amounts of work and power) relative to when running along a level surface (when the gastrocnemius contracts nearly isometrically and generates high levels of force, but almost no work or power). In eels, it seems that the mechanical behavior of the axial musculature shifts to some degree when the external environment changes (as suggested by differences in timing, duration and intensity of activity), but that the animals also face limited performance capacity on land (as shown by low overall locomotor velocities) when using a musculoskeletal system designed for aquatic propulsion.

Further work, examining more muscles within a given locomotor system (for example, muscles acting about the ankle, knee and hip within a limb) as an animal shifts speed, gait or environment is necessary to test more thoroughly the hypothesis that patterns of recruitment might also shift to accommodate gross changes in locomotor function. As we continue to examine muscle function under more dynamic and varied conditions, we can hope to understand better the functional breadth of muscles and how muscle-tendon systems are integrated to permit gross changes in function, both of which are critical to our understanding of the evolutionary design of musculoskeletal systems.

The authors thank W. Corning for his able assistance in the experiments on the mallards, B. Tobalske for helpful comments on an earlier draft of the manuscript and T. Roberts for the use of a modified version of his data for running turkeys. This work was supported in part by grants from the NSF (IBN-9723699 to A.A.B.) and the NIH (NRSA 1 F32 AR08559-01 to G.B.G.).

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