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The Influence of Muscle Physiology and Advanced Technology on Sports Performance

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Key Words

biomechanics, modeling and simulation, muscle properties, optimization

Abstract

Muscle mechanical output such as force and power are governed by highly nonlinear intrinsic muscle properties associated with different muscle fiber types and are influenced by training and age. Many of the interactions between these properties pose trade-offs such that an individual's anthropometrics and muscle morphology may allow an athlete to excel in one sport but not in others. Advanced modeling and simulation techniques are powerful tools to gain insight into performance limits, optimal equipment designs, and mechanisms that may lead to injury. Recent technological innovations have produced faster running tracks, bicycles, speed skates, and swimming pools. This review discusses the influence of intrinsic muscle properties in sports and how advanced technology can be used to extend the limits of human performance.

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INTRODUCTION

For centuries, athletes have sought to maximize athletic performance by increasing human strength, speed, and power and by identifying equipment and training techniques that improve performance. The neuromuscular and musculoskeletal systems are exceedingly complex and are governed by highly nonlinear intrinsic properties, which become more complex when they interact with sports equipment and the environment. Intrinsic muscle properties and their influences on muscle force, power and efficiency, and metabolic capacity limit human performance. However, as our understanding of muscle physiology and biomechanics of human movement expands, improved training techniques that increase muscle strength and endurance and advances in equipment technology have allowed athletes to set new standards in optimal performance. Faster running tracks, bicycles, speed skates, and pools are a few examples that have been optimized to extend the limits of human performance. Advanced modeling and simulation techniques have also been used to gain insight into performance limits and to identify mechanisms that may lead to injury. In this review, we highlight some of the fundamental physiological factors and recent technological innovations that have influenced athletic performance.

THE MUSCULOSKELETAL SYSTEM

Generating muscle force and power are essential for meeting the mechanical energetic demands in a given sport. However, anthropometrics and muscle morphology may allow an athlete to excel in one sport but not in others. For example, good sprinters are rarely good marathon runners and tall athletes do not make for good gymnasts. There are a number of factors that contribute to an athlete's performance in a given sport, and many of these factors are linked to the structure and functional capacity of individual muscles. A number of excellent papers and book chapters have been written about muscle properties (see citations throughout for references). Thus, the purpose of this next section is not to provide an exhaustive review of the topic but rather an overview of those aspects of muscle physiology that are important for sports performance.

Intrinsic Muscle Properties

The mechanical output by skeletal muscles is influenced by several fundamental intrinsic muscle properties that govern muscle force and power output (**Figure 1**) (for reviews see References 1–3). The force-length relationship describes the link between the maximum isometric force attainable at a given muscle fiber length (4, 5). For each muscle, there is an optimal fiber length for force production, and peak force declines when a muscle is operating at lengths that are shorter or longer than optimal (**Figure 1*a***). In addition to active force-length properties, muscles also exhibit passive elastic properties when stretched beyond their optimal length (4). Consequently, the total force-length properties of muscle result from the active and passive components.

The force-velocity relationship describes the link between force development and the rate of change in the muscle fiber length (6, 7). As shortening velocity increases, the capacity of a muscle to produce force declines exponentially to zero at the muscle's maximum shortening velocity (**Figure 1*b***). In contrast, when a muscle is actively lengthened, the force developed by the muscle increases with increasing speeds of lengthening until a critical speed is reached and the force becomes constant (**Figure 1*b***).

Another important intrinsic muscle property relates the timing of muscle activation and deactivation to muscle force development and relaxation. When the nervous system recruits a muscle fiber to produce force, there is a delay between when the muscle fiber is excited and when force

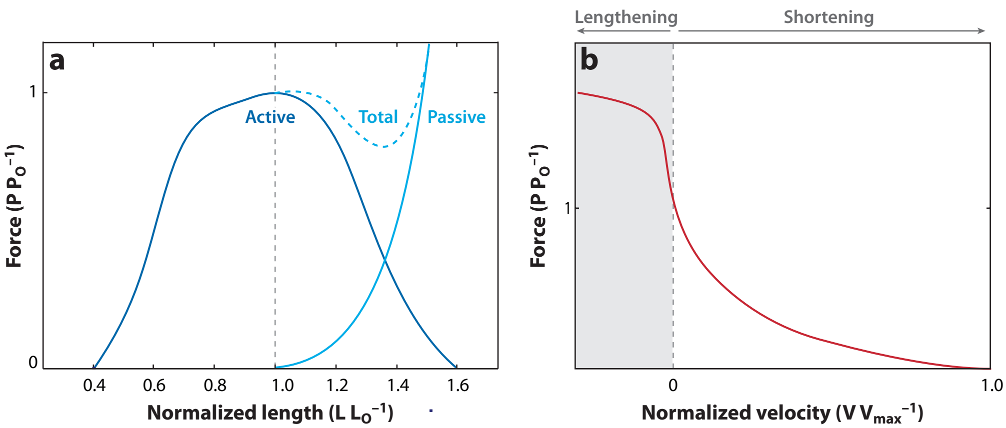

Figure 1

Intrinsic Muscle Properties. (*a*) Normalized active and passive force-length curves for muscle. Maximal isometric active muscle force ($P/P_0 = 1$) is generated when a muscle is at its optimal length ($L/L_0 = 1$) and decreases when the muscle is either shorter or longer than this length. Passive force is developed when a muscle is stretched beyond its optimal length. The total isometric force-length relationship is described by the sum of the active and passive force-length curves. (*b*) Normalized force-velocity curve for muscle. Muscle force decreases exponentially as the velocity of shortening increases and falls to zero when the muscle reaches its maximal shortening velocity (V_{max}). When a muscle is actively stretched, muscle force exceeds the isometric force but only over a limited range.

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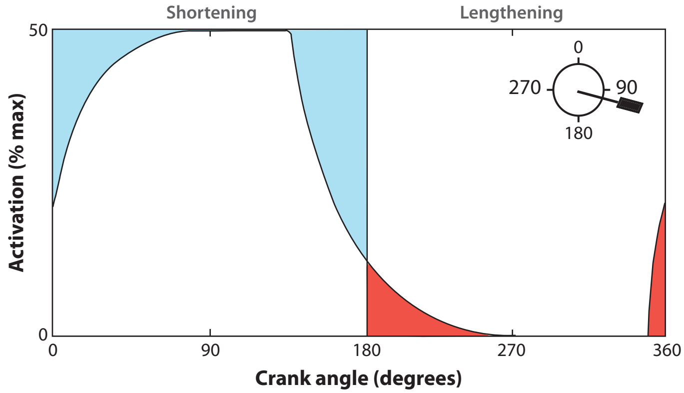

Figure 2

Hypothetical influence of muscle activation and deactivation dynamics on the potential of a muscle to do mechanical work in cycling. Muscle excitation at 50% of maximum occurs with an onset at 350° and ends at 138° in the crank cycle. Blue areas represent potential positive work that could not be achieved as the muscle activates, whereas red areas represent negative work that is generated as the muscle deactivates. The inset shows the orientation of the crank arm at 110° relative to top dead center.

begins to develop (muscle activation). Similarly, when the muscle excitation stops, there is a delay in force decline (muscle deactivation). The delays are due primarily to calcium dynamics and cross-bridge attachment and detachment (for more detail see Reference 3). Because of these delays, there will always be a trade-off between maximizing positive and minimizing negative muscle work during cyclic movements, as the muscles cannot be turned on and off instantaneously (**Figure 2**). As a result, this important muscle property can have a significant influence on performance in many sports that involve fast cyclic movements (8).

In addition to the primary intrinsic muscle properties, there are history-dependent properties that also influence the mechanical output from muscles (9–12). History-dependent effects include stretch-induced force enhancement (11, 13, 14) and shortening-induced force depression (2, 15–17). These properties have been identified in individual muscle fibers (e.g., 10, 13, 18), whole muscles in situ (12, 15, 17, 19), and in vivo in single muscles (9) and whole muscle groups (20). However, current experimental protocols required to identify history-dependent effects do not readily allow the evaluation of how they influence dynamic cyclic movements. Therefore, an important area for future research is to determine the level of influence of history-dependent properties on athletic performance and during cyclical movements in general.

Work: the integral of power over time

In situ: muscle test preparation with some or all of the muscle-tendon system intact

In vivo: occurring within a living organism

Concentric action: active muscle force development during shortening

Eccentric action: active muscle force development during lengthening

Activation dynamics: rate at which muscles can develop force following neural excitation

Muscle Work, Power, and Efficiency

In addition to muscle force, there are a number of related quantities, such as muscle work, power, and efficiency, that are important in athletic performance. The amount of work a muscle can perform is a function of force and change in fiber length ($W = F \times \Delta L$). Muscles can generate or dissipate mechanical work, depending on whether they are actively shortening (concentric action) or lengthening (eccentric action), respectively. Theoretically, the capacity for a muscle to do work is equal to its volume or proportional to its mass (21) and thus on a mass-specific basis, would be equal in all athletes. However, factors such as the influence of intrinsic properties or muscle fiber types (discussed below) likely prevent such equality. The influence of the intrinsic muscle properties (especially the activation and deactivation dynamics) on muscle work during cyclic contractions has been well characterized in animal studies using in situ work loop techniques (22), which are

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formed by plotting force versus length change, with the area enclosed by the loop representing the net work done by the muscle. In situ work loop studies have been an effective means for examining muscle properties such as power, efficiency, and fatigue (23–26). In vivo work loops have been used to differentiate between muscles that function as springs, that is, they generate high force to stretch tendons but do little work (27, 28), and muscles that function as motors to produce high power output (29–31). Although direct in vivo measurements from human subjects are rare, a recent review of cycling studies suggests that this experimental paradigm may be analogous to the work loop technique in its ability to characterize the complex interactions between the various intrinsic muscle properties during cyclic movements (32). Recent simulation studies from our group that have highlighted the importance of activation and deactivation dynamics (8) and shortening duration (33) on power output in cycling support this conclusion.

In many sports, such as sprinting or skating, it is likely that muscle power rather than muscle work is important for performance. Muscle power (the product of muscle force and velocity) is the rate at which muscle work is done. Therefore, greater power output can be achieved by increasing muscle force and /or shortening velocity. However, due to the intrinsic force-velocity relationship, as shortening velocity increases, the ability to generate force decreases exponentially (**Figure 3**). Thus, there is an optimal muscle velocity to generate maximal power, which occurs at approximately 30% of the muscle's maximum shortening velocity (7, 34). Animal studies have measured maximal power output from vertebrate skeletal muscles to range from 250–400 W kg^{-1} during cyclic contractions (35–37), and muscle power as high as 530 W kg^{-1} has been predicted for the pectoralis muscles in quail during take-off flight (29).

In endurance sports that require prolonged athletic output and are aerobic in nature, muscle efficiency is an important physiological factor. In general, muscle efficiency is defined as the ratio of mechanical work output to metabolic energy input. The relationship between muscle efficiency and shortening velocity is similar to that of muscle power and velocity. As shortening velocity increases, so does the rate of energy consumption (38) (**Figure 3**). There is initially an increase

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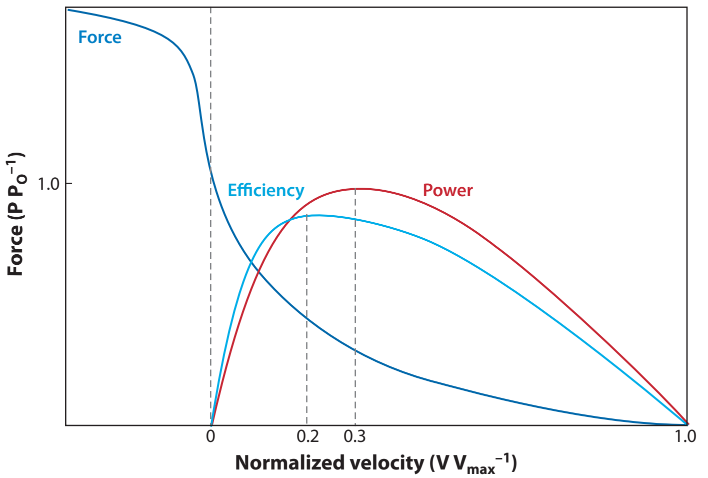

Figure 3

Muscle efficiency (mechanical work output relative to metabolic energy input) and muscle power (the product of muscle force and velocity) vary with shortening velocity. Maximum efficiency is achieved at approximately 20% of the maximal shortening velocity (0.2 V_{max}), whereas maximal power is developed at approximately 0.3 V_{max}. Both efficiency and power are zero when the muscle is contracting isometrically or at its maximal shortening velocity.

in muscle efficiency as the shortening velocity increases, which peaks at ~20% of the muscle's maximum shortening velocity (38) and then begins to decrease. Because peak muscle efficiency and power output do not occur at the same shortening velocity, there is an intermediate velocity that optimizes these two important factors.

Influence of Intrinsic Muscle Properties on Sports Performance

From the preceding discussion, it is clear intrinsic muscle properties have a significant influence on muscle mechanical output. Further, these properties are common to all vertebrate muscle and therefore shared by all athletes. Below are a few examples of how these properties are likely to influence performance in different sports.

In sports that include activities such as running and jumping, an athlete's muscles often undergo eccentric followed by concentric length changes, which are referred to as stretch-shortening cycles (SSCs) (**Figure 4**). A number of studies have shown that SSCs enhance the force, work, and power output during the shortening phase of the SSC (39–41). The mechanisms underlying this enhancement have been attributed to a combination of intrinsic muscle properties (stretch-induced force enhancement and activation/deactivation dynamics), mechanical muscle properties (elastic energy stored in muscle structures), and neural modulation (stretch reflex). However, there remains some debate as to the relative contribution of each mechanism (for review see Reference 42). For example, several studies suggest that additional elastic energy stored and released during the SSC maximizes the mechanical power output measured during running and countermovement jumps (39, 43, 44), whereas others suggest the improved performance is due to the increased time for muscle activation (45). Purely eccentric actions also occur in sports to dissipate energy and prevent joint angles from reaching their anatomical limits, such as during landing following a jump in gymnastics (46), and these act to protect the joints, with the amount

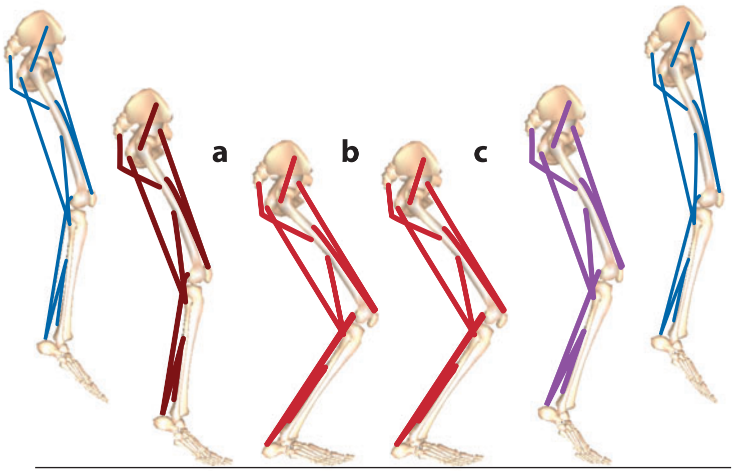

Figure 4

Animation of a drop jump highlighting the phases of the stretch-shortening cycle, which enhances muscle mechanical output. (*a*) Eccentric phase: muscles that are actively stretched develop high forces, store elastic energy, and elicit a stretch-reflex activation response. (*b*) Amortization phase: the time between eccentric and concentric phases, which must remain short or much of the enhanced muscle output is lost. (*c*) Concentric phase: muscles shorten with high force and elastic energy return, which increases muscle work and power output.

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PLYOMETRIC EXERCISES

Plyometric exercises are an effective training technique to develop increased muscle strength and power for sports in which speed and explosiveness are essential (e.g., sprinting, gymnastics, track cycling) (48, 49). Plyometrics utilize stretch shortening cycles (SSCs) (**Figure 4**) that involve mechanical (high eccentric forces, storage and release of elastic energy) and neurological (stretch-reflex activation) mechanisms to increase muscle recruitment and to enhance muscle force and power output (see previous section). A key element of plyometric exercises is the amortization phase, which is the time between the eccentric and concentric phases. If this phase is too long, the benefit from the elastic energy storage and the stretch-reflex response is lost (50, 51). Most studies agree that plyometric exercises are an effective method for increasing muscle force and power output (52, 53); however, the specific mechanisms that contribute to the increases are not well understood. Studies have suggested that increased neural drive (54), improved coordination (55–58), and changes in muscle stiffness characteristics (59–61) may play important roles.

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of eccentric activity dependent on the landing stiffness (47) (for a review of landing biomechanics see Reference 46).

Alternatively, a number of sports maximize the energy produced by muscles through concentric contractions, while they minimize the energy absorbed by eccentric actions. Cycling provides a clear example. Cycling allows the rider to maximize speed and power through modifying the bicycle-rider setup (62) to take advantage of intrinsic muscle fiber length-velocity relationships. Force production and power output during cycling is almost exclusively due to concentric action. However, the amount of negative muscle work generated is pedaling-rate dependent (63, 64). Maximum power output in pedaling has been experimentally measured to occur at pedaling rates near 120 rpm (65). However, during submaximal pedaling, most cyclists prefer pedaling at rates near 90 rpm (e.g., 66, 67). Because the average shortening velocity of the major power-producing muscles is presumably slower when pedaling at 90 rpm compared with 120 rpm, the following question arises. Why don't cyclists increase their pedaling rate to move up the power-velocity curve to achieve more power output for the same muscle activation level (**Figure 3**)? Neptune & Herzog (63) showed that there is a correlation between negative muscle work and the pedaling rates preferred by cyclists (near 90 rpm) and that the cyclists' ability to effectively accelerate the crank with the working muscles diminishes at high pedaling rates owing to increased negative muscle work. This result has important implications for efficiency. Pedaling at rates greater than 90 rpm adversely affects gross muscular efficiency because any negative muscle work would have to be overcome by additional positive work to maintain a given power output. Thus, preferred pedaling rate selection and cycling efficiency appear to be strongly influenced by activation and deactivation dynamics (**Figure 2**) (8). This is supported by the fact that the average pedaling rate for nearly all cycling hour records (i.e., the record for the longest distance traveled in one hour on a bicycle) has been between 90 and 105 rpm (68), which is far below the pedaling rate of 120 rpm at which maximum power output is generated on a bicycle (65).

Fiber Types

Vertebrate skeletal muscle fibers are grouped into three main fiber types: Type I, slow-oxidative (SO), Type IIa, fast-oxidative glycolytic (FOG), and Type IIb(x), fast-glycolytic (FG) (for reviews see References 1 and 69). Slow-oxidative fibers are fatigue resistant and are commonly recruited for long-lasting movements such as slow locomotion (1, 70, 71). However, SO fibers have a lower

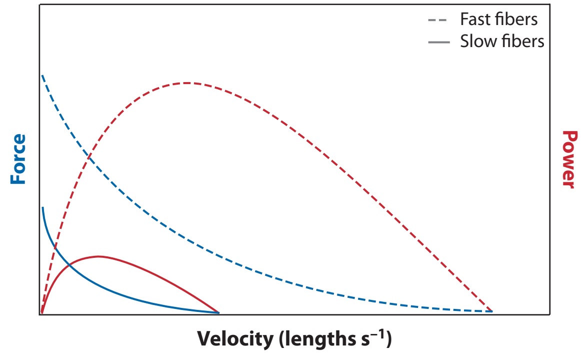

Figure 5

Force-velocity and power curves for fast (*dashed line*) and slow (*solid line*) muscle fibers. Fast muscle fibers generate higher isometric forces and produce more power than slow muscle fibers.

peak force and power output compared with faster fibers (**Figure 5**). Fast-glycolytic fibers are capable of producing higher peak force and have greater power output than SO fibers owing to their rapid contraction speed (1, 69, 72). But FG fibers are quickly fatigued as a result of metabolic acidosis (lactic acid buildup caused by the rapid breakdown of glycogen) and therefore can be active only for short periods of time. FOG fibers are on the spectrum between the slow, fatigue-resistant SO and the rapid, high-force generating FG fibers. For our discussion, FG and FOG are considered fast-twitch and SO are considered slow-twitch (for complete reviews see References 1, 69, and 73).

The proportion of fast- and slow-twitch muscle fibers can vary between individuals and has been associated with athletic performance. For example, in mixed fiber muscles, a sprinter may have up to 75% fast-twitch fibers, whereas a distance runner may have 75% slow-twitch fibers in the same muscle (74). Fast-twitch fibers produce higher forces, and the optimal power output occurs at shortening velocities up to fourfold higher than that of slow-twitch fibers (**Figure 5**). Therefore, maximal power output can be substantially higher (72). However, slow-twitch muscle fibers have a higher efficiency at lower shortening velocities and are more economical and beneficial in endurance events (70).

Although many sports require both power and endurance, and therefore a balance between slow- and fast-twitch fibers, selectively training muscles for a preferential fiber type would be beneficial for task-specific sports. A number of studies have examined the effects of strength training on skeletal muscle (for review see Reference 75); however, whether muscles can substantially change fiber type in response to training remains an area of considerable debate. Several human and animal studies report no change in percent fiber type distribution with training (76, 77), whereas other human studies have found significant changes in fast-twitch fiber type distribution, especially in early stages of training (78–81). Despite these differences, the majority of studies agree that there is greater hypertrophy of fast-twitch muscle fibers relative to slow-twitch muscle fibers in response to resistance training (77, 80, 81).

Muscle Moment Arms

In addition to the intrinsic muscle properties that govern muscle force and power output, musculoskeletal geometry also influences how muscles contribute to a given motion. For example, the muscle moment arm about a joint governs its joint torque capacity and the relationship between

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the joint angular excursion and the corresponding muscle length change. The influence of this relationship has been explored in some animal studies (e.g., References 35, 82, and 83) and is a critical factor in the biomechanics of how animals change posture over a large range of animal sizes (84). Few studies have examined the importance of moment arms in human sports performance. However, a recent study analyzing collegiate sprinters and nonsprinters showed that track and field sprinters had shorter gastrocnemius moment arms and longer muscle fibers (85). Short moment arms mean that for a given angular excursion, there is less muscle length change (and lower shortening velocity), and because their fibers were longer, the length change represents less muscle strain. Thus, shorter moment arms enable sprinters to generate higher forces by operating under more favorable force-length-velocity conditions. This is important for sprinters because generating high ground contact forces is a critical factor in determining maximal sprinting speed (86). In addition, shorter Achilles' tendon moment arms have been associated with better running economy due to high muscle-tendon forces and greater elastic energy storage and return (87).

Because muscle moment arms are inherent in the musculoskeletal system and cannot be altered in a practical way outside of surgical intervention, understanding how musculoskeletal architecture such as altered moment arms influences human performance can be challenging. However, computer modeling and simulation analysis provides a powerful tool for examining these types of questions. For example, we examined the influence of increased muscle moment arms of the hip and knee extensor muscles, which are the primary power producing muscles in cycling (88, 89), on average maximum power that could be generated over a crank cycle at 90 rpm. Using a previously described pedaling model with detailed musculoskeletal geometry (for details see Reference 88), simulations were run in which the average moment arms of gluteus maximus (GMAX) and vastii (VAS) were increased by 10% and 20% relative to nominal values. Optimal fiber lengths and tendon slack lengths were also scaled such that each muscle's fibers experienced similar strains in all conditions. Dynamic optimization was used to identify the muscle coordination pattern that maximized average crank power. The results showed that increasing muscle moment arms by 10% and 20% increased the muscle's contributions to joint torque. Because pedal frequency was constant, joint angular velocities were similar for all conditions, and therefore increases in joint torque produced increases in joint power (**Figure 6**). The net result of increasing GMAX and VAS moment arms by 10% and 20% was an increase in average crank power by 2.4% and 3.4%, respectively. Unlike sprinting, where force output is critical, power output to overcome the external workload (primarily wind resistance) is the critical determinant of performance for cyclists. Thus, this amount of increase would constitute a substantial improvement in performance.

Additional Performance-Limiting Factors

In all sports, there are limiting factors that constrain human performance. For example, in sprinting, the highest speed a runner can achieve is determined by step frequency, contact length (distance traveled during foot contact), and vertical ground contact force (86). As sprint speed increases, ground contact time decreases. Because runners must generate the force needed to support body weight in shorter periods of time, both the peak and average vertical ground reaction forces increase. Ultimately, the ability to rapidly generate these ground contact forces is what limits a runner's top speed (86, 90). This force limitation is apparent when sprinters run through the bend portions of the track, such as in 200 m events. The total ground contact force required in a bend is greater because of the need for generating an additional centripetal force. As a result, sprint speed decreases during the bend portion, which is amplified in indoor competitions in which the bends are tighter and performance is biased by lane number (90).

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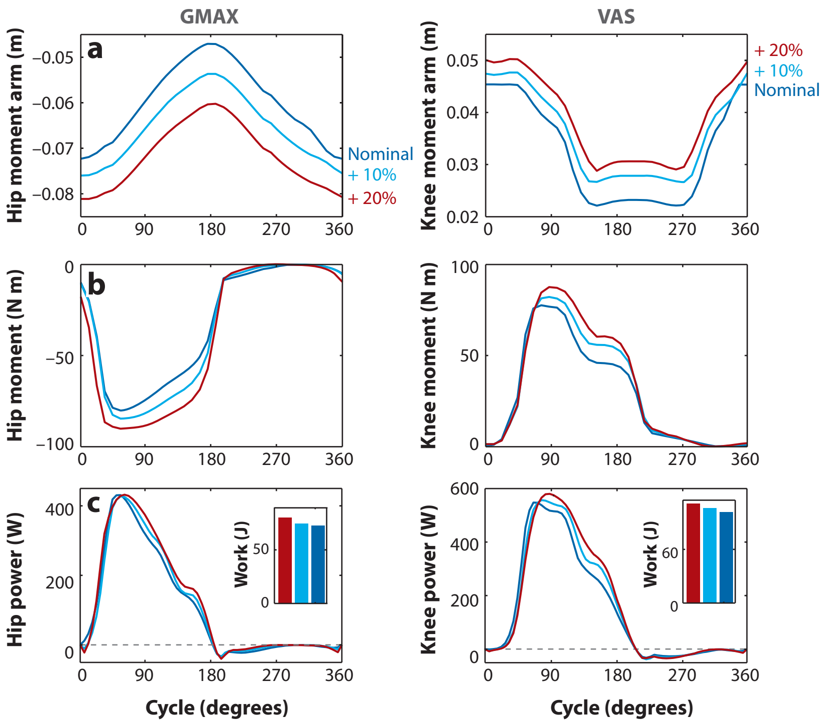

Figure 6

The influence of increased moment arms on cycling performance. (*a*) extensor moment arms for the gluteus maximus (GMAX) and vastii (VAS) during pedaling over the crank cycle (0–360°). Average moment arm lengths during the power phase of the cycle (0–180°) were increased by 10% and 20% relative to nominal values. (*b*) GMAX and VAS hip and knee extensor moments, respectively. Values indicate the percent increase in mean joint moment owing to increased moment arms. (*c*) GMAX and VAS joint power at the hip and knee, respectively. Inset values indicate the work done by each muscle at their respective joints. The net result of increasing the GMAX and VAS moment arms by 10% and 20% was an increase in average crank power by 2.4% and 3.4%, respectively (not shown).

In other sports, the rate at which energy can be produced by muscles limits performance. The two main sources of energy are anaerobic (oxygen independent) and aerobic (oxygen dependent) metabolism. The relative contribution from each energy source depends on task demands, such as power output, duration, and rest periods (91, 92). During relatively low power activities (e.g., moderate jogging, swimming, or cycling), aerobic metabolism is the primary provider of energy (92) (**Figure 7**). As the power output for the activity increases, the aerobic system reaches its maximum capacity to deliver energy or $\dot{V}O_{2\,max}$ (92, 93). Beyond this point, additional energy is supplied by anaerobic metabolism; however, this energy pathway cannot be sustained for long periods of time. Therefore, an athlete's $\dot{V}O_{2\,max}$ sets the upper limit for sustained power output, although factors such as mechanical efficiency and lactate threshold also influence actual performance (for reviews see References 94 and 95). In sports in which endurance is an important component for performance (e.g., distance running, cycling, and cross-country skiing), elite athletes have a $\dot{V}O_{2\,max}$ that is nearly twice that of untrained individuals (**Table 1**) (93). $\dot{V}O_{2\,max}$ has less influence for athletes competing in short duration events, such as sprinting, in which energy is supplied almost entirely through anaerobic metabolism (92).

Aerobic metabolism: produces energy for long, low-intensity exercise

Anaerobic metabolism: produces energy for short, high-intensity exercise

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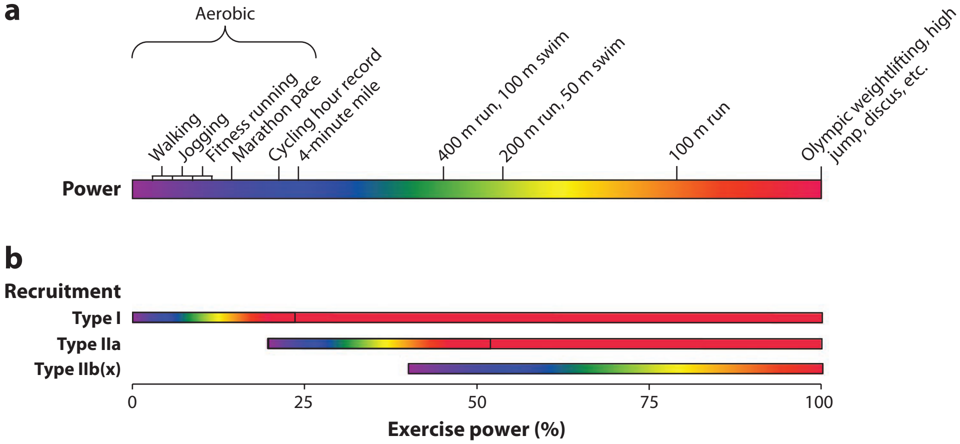

Figure 7

Power output and fiber type recruitment across sporting events. (*a*) Spectrum of percent of maximum power output. (*b*) Spectrum of the fiber type recruitment for the corresponding level of power output. Low-power exercise recruits primarily slow-twitch (type I) muscle fibers. As exercise intensity increases, type I fibers reach their maximum capacity to produce power (*red*) and faster type II and type IIb(x) fibers are then recruited. Figure adapted from Knuttgen et al. (92).

Table 1 Average $\dot{V}O_{2\,max}$ across sports. Data adapted from Reference 93

Sport	Average $\dot{V}O_{2\,max}$ (ml kg*min^{-1})	Range (ml kg*min^{-1})	(n)
Nordic skiing	83	80–85	5
Running (3000 m)	79	78–82	3
Speed skating	78	77–82	3
Orienteering	77	71–84	9
Running (800–1500 m)	75	73–77	5
Bicycling	74	72–80	6
Biathlon	73	70–78	5
Walking	71	67–74	4
Canoeing	70	69–71	4
Alpine skiing	68	52–78	6
Running (400 m)	67	62–69	4
Swimming	66	58–71	6
Ski jumping	62	59–66	3
Rowing	62	56–70	5
Gymnastics	60	49–64	6
Table tennis	59	54–63	3
Fencing	59	51–64	5
Wrestling	57	51–64	10
Weight lifting	56	51–59	3
Untrained	43	38–48	10

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Aging

Aging muscles experience a general loss of muscle mass (sarcopenia), which leads to a decline in muscle performance (for reviews see References 96, 97). Between the ages of 24 and 50, whole muscle mass decreases just 10% (98, 99). However, beyond the age of 50, muscle loss occurs at rates between 0.5% and 1.4% per year (100, 101), leading to ~30% additional loss between ages 50 and 80 (98, 99, 102). Decreased muscle mass is primarily associated with a loss of muscle fibers (99) and a selective atrophy of fast-twitch fibers (99, 103).

Such changes influence all aspects of muscle function important for athletic performance, such as strength and power. Muscle strength in both males and females peaks between 20 and 30 years of age and is largely maintained until 50–60 years of age (103–105). However, consistent with the increased loss of muscle mass and fast-twitch fiber atrophy, beyond 60 years of age, muscle strength decreases at a rate of 15% or more per decade (105, 106). Muscle power begins to decrease earlier, near 40 years of age, and declines more rapidly than strength (107, 108). In addition to the loss of muscle mass, decreased muscle power is also likely due to changes in neural activity (109) and changes in intrinsic muscle properties, such as a reduction in the maximum contraction velocity of fast-twitch fibers (110) and activation dynamics (111). Aging is also associated with a decrease in aerobic capacity or $\dot{V}O_{2\,max}$ that declines ~12% per decade (112).

Training can decrease the rate of muscle strength and power loss associated with aging, with master-level athletes competing well into their 80s. A number of studies have shown that systematic resistance training leads to significant improvements in muscle strength that are independent of age and gender (for review see Reference 97). Continued participation in endurance events has also been shown to help maintain $\dot{V}O_{2\,max}$ (112, 113), with older athletes showing a decrease of only 5% per decade (112), although age clearly influences overall performance. For example, in a study of master-level sprinters (ages 35–88), athletes showed an exponential increase in 100 m dash times with age. The greatest increases in sprint times occurred after 60 years of age (114), consistent with age-related decreases in muscle force (105). As a runner's age increases, better performances are associated with longer distance events (115). Moore (116) showed that the decrease in performance in the 200 m is 0.09 m per second per year, while for a marathon the decrease is only 0.06 m per second per year. Given the atrophy of fast-twitch fibers that comes with age, it is not surprising that many older athletes choose to participate in endurance events that rely more on slow-twitch muscles. For example, in the New York City marathon from 1983–1999, the 50–70+ age group had the highest relative percentage increase in the number of participants (117).

INCREASING PERFORMANCE THROUGH ADVANCED SCIENCE AND TECHNOLOGY

Science and technology are playing an increasing role in helping athletes maximize performance. Advancements have come in the form of new equipment that takes advantage of intrinsic muscle properties or improves force transmission to the environment to advanced modeling and simulation techniques for advanced biofeedback training, equipment optimization, and injury prevention. Below are a few examples of such technological innovations that have revolutionized their respective sports.

Equipment Design

Speed skating—klapskates. In speed skating, higher skating velocities are achieved by reducing frictional losses and increasing power output. Up to 80% of the frictional loss is due to air resistance, with the other 20% due to ice friction (118). To help minimize ice friction losses and to maintain stability when using conventional skates, ankle plantar flexion is suppressed near the end of the power stroke (119). In the early 1980s, van Ingen Schenau and colleagues observed that the mechanics of the power stroke in vertical jumping were very similar to the power stroke used in speed skating (119). However, unlike speed skating, jumpers used increased plantar flexion to further extend the power stroke. This led to the development of the klapskate, which allowed for plantar flexion by using a hinge between the shoe and blade. This innovation enabled the blade to remain flat on the ice while the ankle is extending during the entire power stroke.

The new klapskate design revolutionized the sport of speed skating, allowing skaters to achieve 5% faster times compared with conventional skates (119). The increase in speed was due to an increase in work done by the leg per stroke and the stroke frequency relative to conventional skates (120), which also resulted in improved efficiency (119). Interestingly, the majority of the increase in power came from an increase in work at the knee rather than the ankle (120). Thus, the major advantage of the klapskate was not increasing power output by the plantar flexors but rather enabling the knee extensors to generate greater force and more mechanical work. Following its acceptance in international competitions in 1997, every speed skating world record was broken at the 1998 Nagano Olympic Games by skaters using the klapskate (**Figure 8*a***). However, the full benefit of the klapskate may yet to be realized, as both experimental (121) and computer simulation (122) analyses have shown that performance is influenced by the hinge position on the kapskate, and that the optimal position varies across skaters. The optimal position depends on factors such as individual anthropometrics, muscle physiology, and skating mechanics, and therefore future research developing subject-specific models to optimize the klapskate may lead to further increases in performance.

Swimming Pool and Swimsuit Designs

A swimmer's maximum speed is determined by the balance of propulsion generated by the swimmer and the resistive forces in the water. Resistive forces include friction, wave, and pressure forces (123). The most significant of these is pressure resistance, which is the result of a pressure differential between the front and rear of the swimmer that causes turbulent flow along the body. The magnitude of the resistance depends on the shape, projected area, speed, and orientation of the body relative to the flow of water. Wave resistance is generated as the swimmer displaces water and forms waves, which results in a loss of kinetic energy. Friction resistance is produced as water passes over the surface of the swimmer and depends on the swimmer's immersed surface area.

In 2008 alone, new world records were set in 29 of 40 (73%) long course swimming events (50 m pool; men's and women's) (www.usaswimming.org). At the 2008 Beijing Olympic Games, world records were set in 21 events, some by substantial margins. For example, the men's 4 × 100 m relay team beat the existing world record by more than four seconds (2.19% decrease) (**Figure 8*b***). The basis for the swimming performance increases was technological advances in pool design and swimsuit technology. Federation Internationale de Natation (FINA) allows Olympic pools to be designed in a manner that dissipates water turbulence to minimize resistive forces. Recent designs have incorporated side gutters to reduce wave turbulence from rebounding across the lanes, wave-dissipating lane dividers, and greater pool depth all aimed at reducing water turbulence so swimmers can achieve greater speeds.

The most significant contributor to the increases in swimming performance occurred in recent advancements in swimsuit technology, which revolutionized the sport with the release of the LZR Racer swimsuit (Speedo, Inc.). The swimsuit was engineered with ultra lightweight, water repellent, flexible fabric with ultrasonic welded seams to reduce frictional forces and contoured

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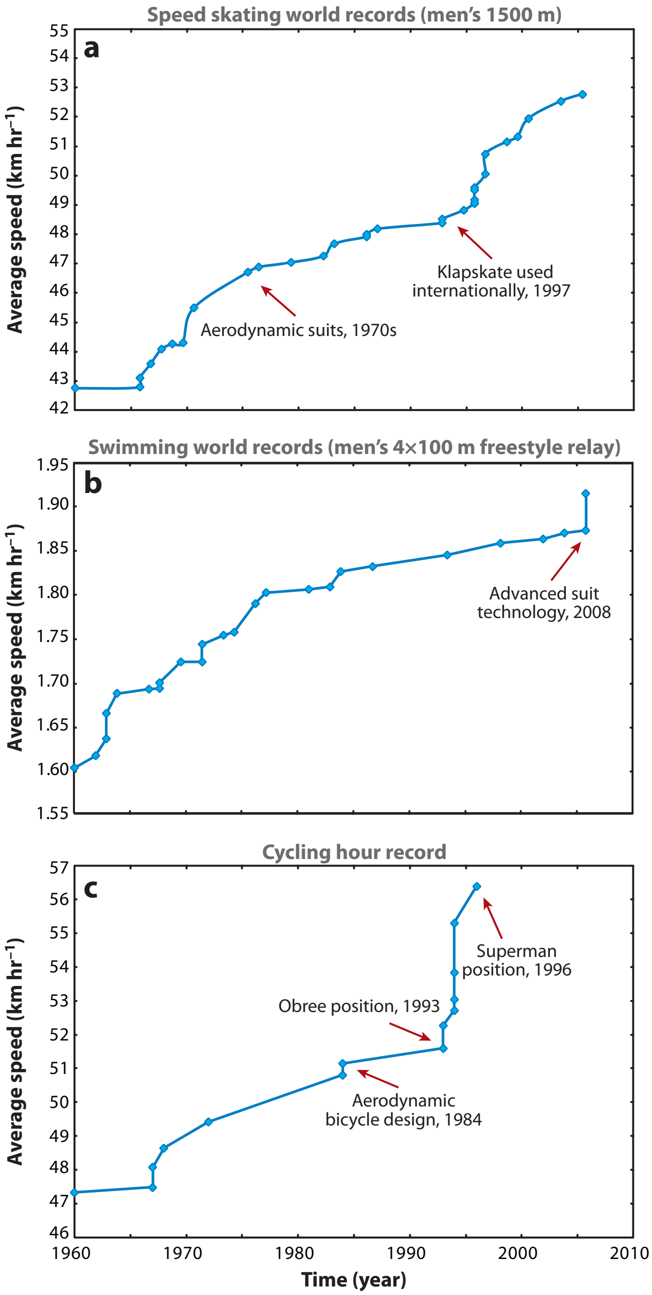

Figure 8

The influence of advanced equipment and technology on world record speeds since 1960. (*a*) Men's 1500 m speed skating. (*b*) Men's 4 × 100 m freestyle swimming relay. (*c*) one-hour cycling record. Arrows indicate when key technological advances were introduced.

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panels that compress the body to assist the swimmer in keeping the optimal body position through the water. Including preliminary heats, 25 world swimming records were broken at the 2008 Olympics, 23 (92%) of which were broken by athletes wearing the new swimsuit. In addition, athletes wearing the new swimsuit won 94% of the gold medals, 89% of all medals, and every event in men's swimming competition (**www.speedo.com**). The clear impact these new suits have had on swimming performance has prompted the governing body of swimming (FINA) to institute new rules regarding which swimsuits can be worn in competitions. The full extent of the rule changes will be based on scientific evidence from ongoing research aimed at understanding the biomechanical impact these suits have had on the sport (FINA Dubai Charter, 2009).

Tuned track: track stiffness is optimized to reduce foot contact time and increase speed

Tuned Running Track

Similar to the engineering advancements in swimming pools, running tracks have been designed to specifically maximize speed and reduce injuries. A historical example is the tuned track developed by Thomas McMahon and colleagues at Harvard University, which was designed to take advantage of the spring-like intrinsic muscle properties of the leg during running. At the time, athletes and coaches had assumed that harder surfaces were faster than softer surfaces, and it was well known that soft surfaces tend to increase foot contact time, with contact time being inversely proportional to speed (124). However, using a simple damped spring model that described running mechanics remarkably well during foot-ground contact ($\sim$120 m s^{-1}), McMahon showed that for an intermediate range of track stiffnesses, the foot contact time was shorter than on a hard surface (125). This led to the idea of a tuned track that could be engineered within a range of spring stiffness to provide faster running speeds by decreasing foot contact time and increasing step length. In 1977, a tuned track was built at Harvard, and runners improved their times by 2% to 3% in a number of running events, while also providing a 50% decreased incidence of injury due primarily to decreased joint loading at impact (125). A similar tuned track used in the 1980 Milrose Games (Madison Square Garden, New York) set new records in every event but one in the first year, and seven new world records were set in the first two seasons (125).

Further research is needed to identify for which running events a tuned track provides the greatest benefit. A tuned track may produce greater benefits for longer running events, as the shorter foot contact time and greater stride lengths associated with a tuned track add up over longer distances. Additional research is also needed to identify how an individual's running mechanics and muscle properties can be altered to maximize the benefit of tuned tracks to further increase performance.

Cycling Equipment

In cycling, riders must accelerate the crank against frictional and inertial loads. At racing speeds, aerodynamic drag accounts for 90% of the resistive forces the rider must overcome (126). Consequently, cycling technology has focused extensively on reducing aerodynamic drag in an effort to increase speed. Innovations in the aerodynamics of cycling equipment have led to controversy in the cycling community regarding which records truly reflect the cyclists' skill and ability and which records are based solely on engineering design. This controversy is particularly relevant in the pursuit of the cycling hour record.

The cycling hour record is the greatest distance achieved in one hour on a flat circuit course riding a traditional bicycle. Prior to 1984, the International Cycling Union (UCI) rules did not allow any device on a bicycle intended to reduce air resistance (126). The legalizing of equipment innovations that served functional or structural purposes led to the hour record being broken

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six times, with a distance increase of more than 5 km from 1993–1996 (**Figure 8*c***). Additional refinements, including nonconventional riding positions, further increased the world hour record.

To identify the influence of equipment design on cycling performance during the hour record, Bassett et al. (127) developed a mathematical model to calculate the power output of former and current hour record holders, after adjusting for differences in aerodynamic equipment and altitude. Their model accounted for a number of factors, including speed, altitude, bicycle design, clothing, helmet design, body position, height, weight, track circumference, and track surface. As a form of model validation, their model produced comparable results to crank dynamometer field measurements of power output by elite cyclists. Their model predicted that at sea level, the power output generated by the hour record holders from 1967–1996 increased from 370 W to 460 W. Aerodynamic advances in bicycle design and equipment setup accounted for 60% of the increase in the hour record, and physiological improvements accounted for 40% of the improvement (127).

Similar to what has recently occurred in swimming, in 2000 the UCI changed the rules to require that a cyclist's equipment be similar to that used to set the hour record in 1972, in an effort to prevent the hour record from becoming influenced more by technology than by the athletes. Records set between 1972 and 2000 were downgraded to "best hour performances" rather than world records (**www.uci.ch**). Although the UCI has constrained equipment used in pursuit of the cycling hour record, advances in equipment design continue in other cycling disciplines. A number of research studies have sought to improve cycling performance by changing various aspects of the pedaling motion through novel crank-pedal mechanisms and noncircular chainring shapes (e.g., 128–131). Below, we show how computer modeling and simulation techniques can be used to optimize chainring shape to maximize power output.

ADVANCED MODELING AND SIMULATION TECHNIQUES

Biofeedback Training

Another way to improve athletic performance is through the use of computer simulators and biofeedback devices, which have been developed to allow athletes to train in realistic scenarios while providing essential feedback necessary to improve performance. This technology has been used to enhance training in a number of sports, such as cycling (132) and rowing (133, 134). Another example is the bobsled training simulator developed at The University of California at Davis to allow U.S. bobsled teams to train for upcoming Olympics. Inspired by aircraft pilot simulators, the bobsled simulator was developed to improve competitive performance by allowing virtually unlimited runs per day, year-round training, difficult portions of the track to be repeatedly practiced, and the reduction of expenses for travel and equipment transport (135). To maximize the benefits to the user and to generate realistic simulations, the simulator was designed to address the visual, vestibular, tactile, and auditory senses of the athletes. The simulator included a computer graphics interface that could be programmed to simulate virtually any bobsled course in the world, a roll about the longitudinal axis of the bobsled to stimulate the vestibular system, a bobsled cockpit with a steering mechanism that included force-feedback to simulate the ice-runner interaction forces, and realistic auditory cues of traveling down the track. Because all external factors (i.e., friction, aerodynamic efficiency, etc.) could be held constant in the simulator model, driver performance in the simulator can be directly attributed to the enhanced training that increased the driving performance. Although a controlled study on the effectiveness of the simulator was not performed, anecdotally, driver Brian Shimer used the simulator in his training and won a Bronze medal in the four-man bobsled event at the 2002 Olympic Games in Salt Lake City.

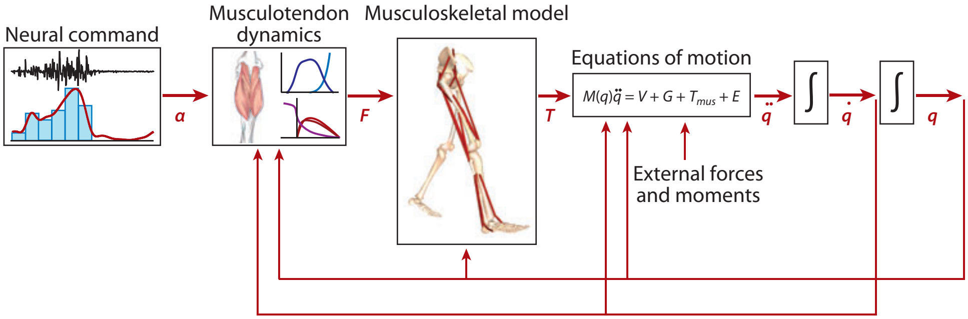

Figure 9

Forward dynamics simulations are analogous to how our neuromotor system functions: Neural control signals excite their corresponding muscles to generate forces that are applied to the body segments, and a corresponding movement results. The dynamic system equations of motion are solved and integrated forward in time to determine the time history of the body segment kinematics (positions and velocities). From the equations of motion, individual muscle contributions to the task performance can be precisely quantified.

Forward Dynamics Simulations

Complex musculoskeletal models and computer simulations are playing an increasing role in sports biomechanics, with applications ranging from optimizing equipment (e.g., 62, 122, 136) and technique (e.g., 137, 138, 139) to identifying potential injury mechanisms (e.g., 140, 141, 142). Muscle-actuated forward dynamics simulations (**Figure 9**) are particularly useful because they allow for the identification of causal relationships between the neural control inputs, specific neuromuscular and musculoskeletal properties, and the task performance (for excellent reviews, see References 143–147). Outside of simulations, understanding such relationships is difficult because of the highly complex and nonlinear characteristics of the musculoskeletal system and dynamic coupling that allows muscles to accelerate joints and segments they do not span, and biarticular muscles can accelerate joints in the opposite direction from their anatomical classification (148). Simulations allow one to investigate how individual muscles accelerate joints and segments, contribute to joint and tissue loading and the required mechanical energetics, function in light of intrinsic muscle properties, utilize elastic energy stored in tendons, and work in synergy to perform a given sporting event. Simulations can also be used to systematically investigate questions such as how altered intrinsic muscle properties or novel equipment designs influence performance without the confounding effect of neuromotor adaptation (e.g., 149, 150).

A number of studies have used muscle-actuated models and simulation to look at impact forces (151–153) and patellofemoral loads (154) in running, ankle sprain mechanisms during cutting movements typical in many sporting events (155, 156), and mechanisms for anterior cruciate ligament rupture during sidestepping movements (141, 157) and downhill skiing (140). Although these simulation results have provided insight into potential injury mechanisms, the challenge remains to identify effective preventative measures to avoid such injuries. Others have used modeling and simulation to understand how muscle strength and coordination influences maximum speed pedaling (89) and jump height (158–160), differences in muscle function between walking and running (161, 162), the optimal bicycle configuration that maximizes power output (62), and which neuromuscular factors determine the optimal pedaling rate in sprint cycling (163) and the preferred pedaling rate (164) in submaximal cycling. These are a just a few examples of how modeling and simulation has been used to investigate various aspects of sport. Below, we give

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two specific examples of how simulations can be used to optimize sports equipment to improve performance and identify sports injury mechanisms.

Eccentric chainring: noncircular bicycle chainring that changes the pedaling kinematics

Cycling—Optimal Chainring Shape

Conventional circular chainrings provide a relatively constant crank angular velocity profile. In contrast, noncircular chainrings can dramatically alter the crank angular velocity profile over the pedaling cycle. The modified velocity profile alters the muscle kinematics during the pedaling motion, and therefore has the potential to provide improved conditions for generating muscle power and increasing performance. We recently developed a detailed musculoskeletal model and simulation of isokinetic pedaling (at 90 rpm) driven by individual muscle actuators (**Figure 10**) that are governed by intrinsic muscle properties (i.e., the force-length-velocity relationships) (**Figure 1**), and we used dynamic optimization to identify the chainring shape that maximized average crank power (33). An eccentric noncircular chainring shape was identified that increased average crank power by 3.0% relative to a conventional circular chainring. The increase in power output was the result of the eccentric chainring shape slowing down the crank angular velocity during the power phase (downstroke), which allowed muscles to generate power longer and thus generate more work (33). Interestingly, the winner of the 2008 Tour de France used a similarly shaped noncircular chainring and was the first rider to win the prestigious race using noncircular chainrings.

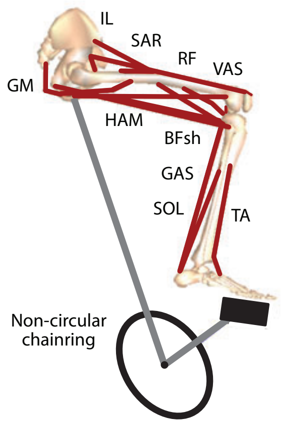

Figure 10

Bipedal bicycle-rider musculoskeletal model used in the chainring optimization (only right leg is shown). The model was developed using SIMM (Musculographics, Inc.) and consisted of nine segments, including a pelvis, two legs, and a crank and pedal system. Each leg consisted of thigh, shank, patella, and foot segments. Standard 175 mm crank arm lengths were used, and the foot segment was fixed to the pedal to represent standard clipless pedals. The resulting dynamical equations of motion were then generated using SD/FAST (Parametric Technology Corp.). The model was driven by 10 muscle groups, including the sartorius (SAR), iliacus, psoas (IL), rectus femoris (RF), three-component vastus (VAS), tibialis anterior (TA), soleus (SOL), gastrocnemius (GAS), biceps femoris short head (BFsh), medial hamstrings, biceps femoris long head (HAM), and gluteus maximus, adductor magnus (GM). Muscles within each group receive the same excitation signal. Dynamic optimization was used to identify the optimal chainring shape that maximized average crank power. A noncircular chainring shape was found that increased power output by 3% at 90 rpm relative to a circular chainring.

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As previously noted, Neptune & Kautz (8) showed that due to activation-deactivation dynamics, there is a trade-off between maximizing the time in the power phase (downstroke) and minimizing the negative work that results while the muscles are deactivating during the upstroke. Therefore, a sensitivity analysis was performed on the activation and deactivation time constants used in the current model. The sensitivity analysis showed that the optimal chainring shape was sensitive to the specific values used. Slower time constants decreased both the chainring eccentricity and average power output owing to an increase in negative muscle work. In contrast, faster time constants resulted in more eccentric chainring shapes as well as an increase in average crank power owing primarily to a reduction in the amount of negative crank work produced following the power phase. As a result, the optimal chainring shape for an individual cyclist most likely varies depending on a rider's fiber type distribution (i.e., activation-deactivation dynamics). For example, an endurance cyclist may have predominately slow-twitch fibers with slower deactivation dynamics, which would result in increased negative work with a more eccentric noncircular chainring shape. Conversely, a cyclist with predominantly fast-twitch fibers (fast deactivation dynamics) would benefit from the more noncircular chainring shape without increased negative work. The mechanism of increasing power output by prolonging the positive work phase is consistent with work-loop studies using animal models showing considerable increases in power output during cyclical tasks by extending the positive work phase (e.g., 165).

Using a similar musculoskeletal model and simulation of pedaling, Umberger et al. (166) showed that a higher percentage of fast-twitch fibers (63%) expended 14% more metabolic energy than subjects with the lowest percentage of fast-twitch fibers (27%) when cycling at the same mechanical power output and cadence. Although fast-twitch muscles expend more energy than slow-twitch muscles at the same cadence, fast-twitch muscles have improved mechanical efficiency at a higher cadence (166). This further highlights the potential influence of fiber type composition on cycling performance.

Running—Identifying Injury Mechanisms

Acute hamstring injuries are common in sports involving sprinting, with one in three athletes reinjuring their hamstring within a year of returning to their sport (167). Despite their prevalence, the injury mechanisms are not well understood. To help identify potential injury mechanisms, muscle-actuated forward dynamics simulations of the swing phase of sprinting were used to assess the influence of running speed on peak strain, maximum force, and negative (eccentric) work in the biceps femoris long head (142, 168, 169), which is the most often injured hamstring muscle during sprinting (170). The analyses showed that the hamstrings undergo a stretch-shortening cycle at the end of swing, with peak hamstring force occurring just prior to peak muscle stretch. An interesting finding was that peak hamstring musculotendon stretch was found to be invariant with running speed. However, since hamstring force output increases with speed, negative musculotendon work also increased, and therefore hamstring injuries during sprinting are most likely related to the eccentric work occurring over repeated sprinting strides that predispose the muscle to injury (171, 172).

The model was further used to assess the influence of muscle coordination of other muscle groups and tendon compliance on hamstring mechanics using a perturbation analysis (169). The analysis showed that the trunk and pelvis muscles have the greatest potential to increase hamstring strain by altering the pelvic tilt. Thus, effective coordination of the trunk and pelvis muscles may be an effective mechanism to reduce the potential for hamstring injury. The analysis also showed that as tendon compliance decreased, hamstring fiber strain and eccentric muscle work increased. Thus, stiffer tendons appear to increase the potential for injury.

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SUMMARY POINTS

1. Intrinsic muscle properties, including the force-length-velocity-activation relationships influence muscle force, power, work, efficiency, and ultimately sports performance.
2. A stretch-shortening cycle is an effective mechanism to achieve enhanced muscle force and power output.
3. Maximum muscle power and efficiency do not occur at the same speed, and therefore a compromise is often needed in sporting events.
4. An individual's anthropometrics and muscle morphology may allow an athlete to excel in one sport but not in others.
5. Muscle mass, strength, and power all decrease with age. However, training methods can suppress the rate of muscle strength and power loss with age.
6. Recent technological innovations have produced faster running tracks, bicycles, speed skates, swimsuits, and pools to expand the limits of human performance.
7. Advanced modeling and simulation techniques are powerful tools to gain insight into performance limits, optimal equipment designs, and mechanisms that may lead to injury.

FUTURE ISSUES

1. Further studies are needed to understand the biomechanical and neurophysiological mechanisms that limit human performance and to understand how detailed measurements of an individual's neuromusculoskeletal system (e.g., muscle force, strength, power-generating capacity, muscle coordination, and fiber type recruitment) can be used to make subject-specific recommendations for training, equipment, and rehabilitation for the individual's specific sport.
2. Injury mechanisms are not well understood in a number of sports. Future work is needed to understand what factors predispose an individual to injury.
3. More accurate musculoskeletal models that include subject-specific anatomical and physiological parameters; joint kinematics; body segment inertial characteristics; and muscle models that accurately characterize intrinsic muscle force–generating properties, geometry, and architecture; and history-dependent phenomena, such as force depression and enhancement, are needed to improve the fidelity of modeling and simulation predictions. Such enhancements will improve the ability of biomechanists, physical therapists, and coaches to make subject-specific recommendations regarding rehabilitation, training, and equipment selection for optimal performance.
4. Discussion is needed to provide rationale for what technological advancements should or should not be allowed in athletic competitions. For example, should advanced aerodynamic engineering be allowed in cycling or swimming events or lower-limb amputees with energy-storing prosthetic devices be allowed to compete with nonamputees in running events?

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review. The views expressed in this article are those of the authors and do not reflect the official policy or position of the United States Air Force, the Department of Defense, or the United States Government.

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2. An excellent explanation of how intrinsic muscle properties contribute to mechanical output.

7. Classic work defining intrinsic muscle properties.

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