INTRODUCTION

A common idea in motor control is the use of primitives to control complex tasks. Bernstein (1967) posited that because of the large number of degrees of freedom involved in multijoint movement (including muscle states as well as kinematic states), control must be hierarchical. Understanding how a muscle-coordination pattern required to execute one task changes to execute another may give insight into the way existing motor patterns serve as ‘‘initial guesses’’ in the learning of new tasks (Greene 1982) and into the features common among the patterns (the ‘‘primitives’’) (Giszter et al. 1993; Mussa-Ivaldi et al. 1994). Coexcitation of muscles (i.e., partitioning of muscles into a group, called a ‘‘functional muscle group’’) (Jacobs and MacPherson 1996; Raasch et al. 1997) is one possible primitive and is a common concept in motor control (McCollum 1993; Zajac and Gordon 1989).

Functional muscle groups have been identified in intact animals during walking and postural balance (Engberg and Lundberg 1969; Macpherson et al. 1986; Rasmussen et al. 1978). Two groups alternating in excitation with one another (called a pair of alternating muscle groups) (Raasch et al. 1997) are often anatomic antagonists (Bradley and Smith 1988; McCollum 1993) though not necessarily (Jacobs and MacPherson 1996).

Alternating muscle groups are a basic tenet in the concept of pattern generation of rhythmic locomotor movements (Grillner 1975, 1981; Shik and Orlovsky 1976). Electromyographic (EMG) recordings from animal locomotor preparations have been shown to be compatible with the idea of grouped-muscle control (Rossignol 1996). In ‘‘fictive’’ locomotion, the basic alternation of neural output to the muscle groups even can be generated in the absence of movement (Grillner 1988; Grillner and Zangger 1979). To respond to disturbances and changing task demands, however, movement and other feedback are believed to be critical to locomotor pattern modulation (i.e., gain and phase modulation of muscle groups) (Pearson 1993; Rossignol et al. 1988). For example, the cat ‘‘locomotor pattern generator’’ could produce a faster walking speed or a higher limb power output at the same speed (e.g., to walk upslope) by increasing the neural excitation to the muscle groups without changing their phasing. This can be achieved by increasing the overall tonic drive to the spinal cord through supraspinal descending or unspecific afferent signals (Grillner 1975, 1981, 1988; Shik and Orlovsky 1976). Changing the gain of one or more groups may be a sufficient control strategy for responding to disturbances (Forssberg 1979). At other times, changing muscle phasing is required as well, such as to switch to a different gait (Grillner 1981; Shik and Orlovsky 1976).

In humans, elucidation of locomotor muscle groups from the large number of degrees of freedom involved in multijoint movement (including muscle states as well as kinematic states), control must be hierarchical. Understanding how a muscle-coordination pattern required to execute one task changes to execute another may give insight into the way existing motor patterns serve as ‘‘initial guesses’’ in the learning of new tasks (Greene 1982) and into the features common among the patterns (the ‘‘primitives’’) (Giszter et al. 1993; Mussa-Ivaldi et al. 1994). Coexcitation of muscles (i.e., partitioning of muscles into a group, called a ‘‘functional muscle group’’) (Jacobs and MacPherson 1996; Raasch et al. 1997) is one possible primitive and is a common concept in motor control (McCollum 1993; Zajac and Gordon 1989).

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studies of walking is difficult because of the complexity of the task. Nevertheless studies of supported treadmill stepping in spinal-cord-injured patients have suggested the existence of pattern generators in the human spinal cord (Barbeau and Rossignol 1994; Calancie et al. 1994; Dietz et al. 1995; Rossignol and Barbeau 1995; Rossignol et al. 1996). The mutability of human locomotor patterns has been examined in split-treadmill walking, where different belt speeds cause ankle flexors to be excited longer because a longer swing phase of the leg on the slower belt is needed (Dietz et al. 1994). Also in backward walking, uniarticular knee extensors remain excited in the support phase (as in forward walking) (Winter et al. 1989), while bifunctional thigh muscles switch in phase relative to the two transitions between stance and swing (heel-strike and toe-off in forward walking; toe-strike and heel-off in backward walking) (Thorstensson 1986). Thus it appears that some parts of the locomotor pattern can be modified with some muscles more dependent on task directionality than others.

Pedaling is a bipedal locomotor task well suited to the identification of functional muscle groups and propulsion strategies in humans. Both pedaling and walking are cyclical at about the same frequency (~1 Hz) (Coast and Welch 1985; Winter 1983). Both tasks require the legs to alternate in flexion and extension with most of the propulsive energy generated in extension. Both demonstrate the same phase-dependent modulation of reflexes (Brooke et al. 1992; Brown and Kukulka 1993; Yang and Stein 1990). Ergometer pedaling is, however, different from walking in other ways, some of which are advantageous to the study of legged propulsion and muscle coordination. Balance is not a factor in seated pedaling, so muscle-coordination patterns applicable to propulsion per se should dominate. In fact, experiments to elucidate the pattern-generating properties of locomotion in animals (Forssberg et al. 1980; Grillner 1981; Grillner and Zangger 1979) and infants (Forssberg 1985) also have emphasized propulsion coordination (cf. balance coordination). Because pedaling is a kinematically constrained task with fewer degrees of freedom than walking, it is easier to simulate with a computer model and more amenable to experimentation. Still, pedaling is sufficiently complex that muscle coordination is not trivial. For example, because of dynamic interactions among the segments (Zajac and Gordon 1989) and the constraints of the closed linkage in pedaling (which also occurs in the double-support phase of walking), the actions of individual muscles on the system are not obvious; e.g., the biarticular hamstrings, anatomically classified as a hip extensor and a knee flexor, act to accelerate the knee oppositely, into extension, in the crank downstroke (Raasch et al. 1997). Therefore it is important to account for the complex mechanics of muscle and segments when hypothesizing neural control strategies or attempting to deduce underlying strategies from experimental data.

We have used a computer model of the musculoskeletal system, in conjunction with experimental work, to begin to characterize the essential neural-control elements required for pedaling propulsion based on the biomechanical requirements of the task. In an experimental and theoretical study of maximum-speed start-up forward pedaling, Raasch et al. (1997) have shown that a controller constrained by lower limb muscles organized into four groups performs as well (within 4% of maximum speed during start-up) as an unconstrained controller where each muscle is excited independently from the others (Raasch et al. 1997). Nearly equal performance is achieved because the biomechanics of the task, specifically, the individual muscle contributions to crank and limb propulsion, is nearly replicated with control of the four muscle groups. In fact, the control strategy can be simplified further because it was found that each group alternates in phasing with one other group. Thus the four groups can be arranged into two pairs, with only one signal controlling each pair because the two groups in each pair alternate due to their nearly opposing biomechanical functions.

In this simple control scheme of pedaling, one pair of alternating muscle groups produces the energy needed to propel the crank through limb extension (the uniarticular hip and knee extensor muscles, EXT) and flexion (the uniarticular hip and knee flexor muscles, FLEX), with some energy to accelerate the limb segments first. The other pair facilitates the transfer of energy to the crank produced by the other muscles and also produces energy to propel the crank directly, near the end of extension and during the limb transition from extension to flexion (the hamstring and ankle plantarflexor muscles, HAM/TS) and near the end of flexion and during the flexion-to-extension transition (the rectus femoris and ankle dorsiflexor muscles, RF/TA). A muscle transfers energy by essentially acting as a rigid link to constrain the acceleration of limb segments (though it also may be simultaneously absorbing or generating energy, and so may not be strictly isometric). For example, plantarflexors can constrain ankle motion in downstroke so that acceleration of the shank by nonankle muscles now also will accelerate the foot and, by intersegmental coupling (Zajac and Gordon 1989), the crank.

The biomechanical functions performed by the four muscle groups (Raasch et al. 1997) (see preceding text) have been the basis for analysis of EMG patterns generated by neurologically healthy and impaired individuals during pedaling. Kautz and Brown (1998) found that the degradation of pedaling performance measured in older adults with poststroke hemiparesis was related to abnormalities in the execution of specific biomechanical functions, as evidenced by changes in EMG timing. In a study of forward pedaling at different cadences by young healthy adults, Neptune et al. (1997) concluded that the phasing of the functions remain unaltered, although a few muscles under specific pedaling conditions may contribute to more than one biomechanical function. These studies suggest, therefore, that while the phasing of a biomechanical function (e.g., leg extension) remains constant for a given pedaling task, a muscle’s contributions to it may depend on the specific pedaling condition. Nevertheless each muscle group, as defined and studied here, can be associated with one primary biomechanical function. Thus coordination of biomechanical functions, which may serve as control primitives for pedaling (Ting et al. 1999), can be revealed by studying functional muscle-group control of pedaling.

The objective of this study was to use computer simulations to ascertain how adaptable the four muscle groups or, equivalently, the biomechanical functions are to pedaling under a variety of conditions. Pedaling at different cadences, with different workloads, and in different directions (forward and backward) was studied because these conditions, when imposed on locomoting animals, have led to the development of principles of locomotion in animals (Buford and Smith 1990; Grillner 1981). Pedaling at a constant crank angular velocity and at a steady cadence (i.e.,
and with high metabolic energy efficiency, also was studied to obtain insight into the role of the muscle groups and to assess the ability of a simple controller to provide sufficient richness for a range of pedaling goals. Finally, to assess how the basic pattern could be adapted to a significantly altered loading condition, pedaling with one leg was studied because this task is similar kinematically but different biomechanically from a two-legged pedaling task (i.e., the contralateral nonpedaling leg no longer provides crank propulsion when the pedaling leg is undergoing limb flexion).

This work is based on a PhD dissertation by C. C. Raasch (1996).

METHODS

Musculoskeletal model and the four muscle groups

The dynamic musculoskeletal model was identical to the one used to study coordination of muscles for maximum acceleration of the crank from rest (Raasch et al. 1997). Briefly, it consists of two legs rigidly connected by cranks to an inertial and frictional load emulating a Monarch ergometer flywheel with a changeable frictional load. The model includes a state-dependent load so that, like a normal ergometer, the crank can freewheel (decouple from the flywheel) when the total cranking torque drops to approximately zero. When freewheeling occurs, the inertia of the load is reduced ~500-fold (i.e., that of the crank and chain drive system only) and the frictional load to virtually zero. During freewheeling, pedaling may continue although crank rotation lags flywheel rotation. If enough propulsive force again is created, the crank accelerates and impacts the inertia of the flywheel, causing a sudden jerk during recoupling. Each leg of the model is constrained to a parasagittal plane with hip center fixed, and feet attached to the pedal to emulate fixation with cleats or clipless pedals. The dynamic equations of motion of the crank and load, the limb segments, and the muscles are of the general form

\[ \ddot{q} = M^{-1}(q)[R^M(q) \cdot F^M(q, \dot{q}, t^M, a^M) + G(q) + V(q, \dot{q}) + D(q, \dot{q})] \]  

\[ a^M = f(a^M, u(t)) \]

\[ a^M = \begin{cases} [u - a^M] \cdot [c_1, \dot{q}, q + [c_2, \cdot c_3]] & u \geq a^M \\ [u - a^M] \cdot c_2 & u < a^M \end{cases} \]  

where \( q \) is a vector of generalized coordinates (i.e., crank angle, \( q \), right and left pedal angles); \( q, \dot{q} \) are the angular velocity and acceleration vectors with, for example, \( \dot{q}_{\text{ang}} \) (an element of \( \dot{q} \)) being the crank angular velocity; \( M(q) \) and \( R^M \) are the system mass and moment arm matrices, respectively; \( F^M(t, q, \dot{q}, t^M, a^M) \) is a vector of muscle fiber length and activation, respectively; \( F^B(q, \dot{q}, t^B, a^B) \) is a vector of muscle forces and includes the active and passive force-length and velocity properties of muscle and accounts for compliance in tendon and aponeurosis [note: \( t^B \) is a vector of muscle fiber velocities and is imbedded in \( F^M(t, q, \dot{q}) \) since \( t^M = f(t^B, q, \dot{q}) \)]; \( G(q) \), \( V(q, \dot{q}) \), and \( D(q, \dot{q}) \) are vectors of gravity, motion-dependent, and frictional terms, respectively. Nine “muscles” (Fig. 1) provide the forces required to move each leg. Excitation-contraction dynamics (Eq. 2), which describe the relation between neuromuscular excitation \( a(t) \) and muscle activation \( a(t) \), include terms \( c_1 \) and \( c_2 \), which are related to muscle activation/deactivation time constants, with \( c_1 = \tau_{\text{exc}} - \tau_{\text{deact}} \) and \( c_2 = \tau_{\text{deact}} \). Activation and deactivation time constants were 50 and 66 ms, respectively (Winters and Stark 1987).

The nine muscles (Fig. 1) of each leg were partitioned into four muscle groups (Fig. 2A, black bars). The nominal ON/OFF phasing of the groups were derived by averaging the ON (OFF) times of the homologous muscle groups in the right and left legs of the simulated first-cycle of maximum-speed start-up forward pedaling (Raasch et al. 1997). For submaximum speed pedaling, this corresponds to a simple strategy of exciting muscles when they can contribute to crank propulsion. Such a strategy should be sufficient to achieve forward pedaling but not necessarily optimal in any sense. The first cycle was used because it was the closest to 60 rpm (the nominal pedaling cadence). The four groups of each leg were assumed to alternate 180° out of phase with their contralateral counterparts. All muscles in a group were excited at the same intensity level.

A study of the capability of such a four-group control was our primary goal. Nevertheless unconstrained optimizations also were run, with all nine muscles excited independently, as a check to see if the groupings were producing unrealistic constraints on excitation timing and excitation levels. Detailed performance figures for these studies are not included; however, key similarities and differences are noted in the following text.

Different cadences and workloads

Simulations of pedaling at different cadences (60 and 90 rpm) and power outputs (120 and 180 W) in the forward direction were attempted by exciting the four groups with the nominal phasing pattern (Fig. 2A). For any given cadence and power output, muscle groups were excited at the same intensity level because such excitation of groups is the strategy required in maximum-speed start-up pedaling (i.e., excitation of a muscle is maximum during its burst) (Raasch et al. 1997). Thus it was assumed that a reduction in excitation intensity of the groups, each by the same amount, would achieve less-than-maximum crank power output [crank power output = cadence (cycles/s) × workload (energy output per cycle)].

Different pedaling goals

A parameter optimization algorithm (Pandy et al. 1992) was used to determine how the four-group control would need to be modified to
pedal more smoothly or efficiently. The algorithm found the phasing and the level of excitation of each of the four groups that minimizes either the amount of nonsmoothness or metabolic muscular energy consumed. No constraint of alternation of one group with another was imposed (however, see RESULTS). Muscle metabolic energy consumption $E^M$ was calculated from mechanical work and heat production as follows (Schutte et al. 1993):

$$E^M = \int P^H = \int [h^t, i^t, i^H, F^H - F^q]$$

where $P^H$ is metabolic power and $h$ is a Hill-based model of muscle heat production, which includes formulations for maintenance, shortening, and lengthening heat rate. In general, the heat rate increases with activation, muscle force, and fiber velocity (except for very slow lengthening, where it decreases slightly). An initial interval of pedaling allowed for settling of transients. Only the last pedaling cycle was subjected to the steady-state constraints of fixed time per cycle and equal initial and final crank velocity. For each simulation, the deviation of crank angular velocity from the desired cadence and the metabolic muscular energy consumed, each averaged over the last cycle, were calculated

$$J_1 = 1/T \int \frac{q_{crank} - q_{des}}{q_{des}} \quad \text{(Nonsmoothness)}$$

$$J_2 = 1/T \sum_{m} E^M \quad \text{(Average Metabolic Energy Rate)}$$

where $T$ is the last-cycle period and $q_{des}$ equals the desired cadence (60 or 90 rpm). Notice from Eqs. 3 and 5 that the metabolic energy consumed, when averaged over the last cycle, is the average metabolic energy rate in the last cycle. Similarly, Eq. 4 yields the average absolute difference from desired speed over the last cycle. Thus a coordination pattern producing smoother pedaling reduces $J_1$, and a pattern causing higher energy efficiency reduces $J_2$. Other measures of nonsmoothness also could be used, such as functions of jerk (derivative of acceleration) or crank angle residuals (Fig. 2C). However, because crank velocity is part of the state vector, it proved a straightforward quantity to monitor continuously and integrate during optimizations.

The effectiveness of the four muscle groups to achieve forward pedaling with one leg was explored. The four groups were phased with the nominal pattern (Fig. 2A) and excited at the same intensity level. Improvement in performance was explored by changing the relative levels of excitation among the four groups without altering their phasing. In all simulations of one-legged pedaling, the model was modified. One leg and a pedal were removed, and the frictional load was halved from the nominal. Thus the mechanical work performed by the leg over the crank cycle in one-legged pedaling was identical to the work performed by the leg in two-legged pedaling.

FIG. 2. Four muscle groups and their phasing (A), comparison of the nominal pedaling coordination pattern with electromyographic (EMG) data (B), and comparison of model generated and observed pedal crank kinematics (C). A: pattern derived from a simulation of maximum-speed start-up forward pedaling (Raasch et al. 1997) (see METHODS). Uniarticular hip extensors (GMAX) are coexcited with uniarticular knee extensors (VAS) (i.e., the EXT group, or E group) and alternate with coexcitation of the uniarticular hip flexors (IL) and the knee flexor (BFsh) (i.e., the FLEX group, or F group). These groups form the EXT-FLEX pair. Another pair consists of the RF/TA group (i.e., the EXT-FLEX pair with uniarticular posterior thigh muscles [RF] and dorsiflexor muscles [TA]), which alternates with the HAM/TS group (i.e., biarticular anterior (RF) and dorsiflexor muscles (TA)), which alternates with the HAM/TS group (i.e., biarticular posterior thigh muscles (HAM) and ankle plantarflexors [TS]); TS includes both uniarticular plantarflexors (SOL) and gastrocnemius (GAS). Diagram shows phasing of the muscle groups with respect to the crank and its position relative to the seatpost. Crank is vertical at TDC (“top dead center”) and BDC (“bottom dead center”). Downstroke (leg extension) occurs as the crank proceeds from TDC to BDC; upstroke (leg flexion) from BDC to TDC. B: phasing of the groups (black straight bars) compared with EMG phasing (gray bars and lines, mean ± 1 SD) (Neptune et al. 1997, by permission). Height of the bar shows the excitation level of the group or muscle, with the peak EMG level normalized by the peak value from maximum voluntary contractions. Normally, all muscle groups in the simulation are excited at the same intensity level (27% of maximum), with maximum equal to 1 (see scale, right). EMGs were measured at a power output of 250 W; hence the higher level of VAS and SOL. EMG levels for 120 W in Ericson (1986) (case with toe clips) are lower, particularly VAS and GMAX. Averaging the magnitude for the 8 muscles yields a value of 24% for 120 W (Ericson 1986), 31% for 250 W (Neptune et al. 1997). C: comparison of simulation (black line) to experimental kinematic data (gray regions, mean ± 1 SD) (Fregly 1993), measured with identical cadence, power output, and inertial load. Similar data also are seen for 75 rpm in Fregly et al. (1996). Top: crank angle residuals, defined as deviation from linearly increasing crank angle (constant velocity). Crank velocity is rarely if ever reported. Crank residuals closely correspond to our nonsmoothness cost. Bottom: pedal angles, with 0 defined as horizontal and negative as toe downward.
**Backward pedaling**

The feasibility of using the nominal forward-pedaling muscle-excitation pattern (Fig. 2A) to pedal backward was explored. That is, the four muscle groups were phased (Fig. 6A) with respect to limb extension and flexion and the transitions between extension and flexion according to the nominal pattern (cf. Fig. 6A, left; phasing diagram, with Fig. 2A). Muscle groups were excited at the same intensity at a level compatible with the achievement of forward pedaling (see RESULTS). Other attempts to pedal backward used excitation patterns where either the levels of excitation differed among the groups or the phasing of the groups or muscles within a group differed from the nominal pattern.

**RESULTS**

**Nominal cadence and workload**

The simulation was able to pedal forward at a steady 60-rpm, 120-W power level with the excitation level of the four-group control set at 0.27 of maximum. The nonsmoothness cost was 0.685 rpm and the metabolic cost 611 W. The oxygen consumption rate for the nominal 60-rpm simulation, computed by assuming an aerobic metabolism of 20.1 kJ/L O₂ (Astrand and Rodahl 1977) and a baseline/resting VO₂ of 0.3 L O₂/min (no-load pedaling) (Croisant and Boileau 1984), was within 5% of measured oxygen uptake rate (Croisant and Boileau 1984; Swain et al. 1987). The pedaling simulation was very realistic, as judged by graphic display of the motion of the body segments and crank relative to one another. The crank angular velocity was maintained to within 1.2 rpm (1.8%) of the desired crank angular velocity, so that cadence was constant to within ± 0.1%.

The crank and pedal kinematics were similar to those recorded from subjects (Fig. 2C, gray regions) (Fregly et al. 1996). The phasing pattern of the four groups corresponded generally well to the EMG pattern recorded during pedaling (Neptune et al. 1997) (Fig. 2B, gray bars). However, subtle differences between simulation and experimental data exist (see DISCUSSION). Nevertheless if muscles are allowed to be excited independently instead of being constrained into four groups, our musculoskeletal model can replicate the experimental data even better (Neptune and Hull 1998).

**Different cadences and workloads**

Continuous pedaling in the forward direction at the higher cadence (90 rpm) and power output (180 W) was achieved with the nominal phasing pattern (Fig. 2A). Pedaling at the faster cadence or higher power output required, however, a higher excitation intensity (0.349 and 0.365 of maximum, respectively) and cost more metabolic energy J₃ (913 and 823 W). The nonsmoothness cost increased for higher power (1.157 J₃) but decreased for higher cadence (0.538 rpm). Pedaling at other cadence/workload combinations, though not thoroughly studied, also were achieved with the nominal pattern.

**Different pedaling goals**

To maximize smoothness, the intensity of excitation of the four muscle groups had to be changed much more than the phasing of the excitations (Fig. 3A). The excitation levels of the RF/TA and HAM/TS groups had to be increased substantially (50 and 44%, respectively) and the excitation of the EXT group decreased (~25%). During limb flexion, the excitation level of the FLEX group had to be increased (36%). Nonsmoothness cost was reduced from 0.685 to only 0.247 rpm. These changes decreased the crank deceleration at the limb transitions and reduced the peak-to-peak crank velocity variations (from 2 to 1 rpm; Fig. 3B, compare --- with · · ·), but metabolic energy consumption increased (from 611 to 648 W, +5%). Unconstrained optimization with all nine muscles excited independently produced very similar results. Excitation of some muscles in the RF/TA, HAM/TS, and FLEX groups had to be increased (i.e., RF, TA, HAM, IL, BFsh) and excitation of muscles in the EXT group decreased [i.e., VAS, GMAX]. Only very small changes in phasing occurred.

To maximize energetic efficiency, excitation of the four muscle groups also had to be changed much more than their phasing (Fig. 4A). Propulsion was provided almost exclusively by the EXT group through an increase in its excitation level (+85%), although its burst duration was shorter. The FLEX group was not excited anywhere in the cycle, and the excitation levels of the RF/TA and HAM/TS groups decreased substantially (~85 and ~37%, respectively). The metabolic energy cost decreased from 611 to 518 W. Consistent with the decreased use of the RF/TA and HAM/TS groups, peak-to-peak crank velocity variations increased (to 5 rpm) although freewheeling did not occur. With muscles excited independently, a similar emphasis on the use of extensors was seen, with VAS recruited first and then GMAX at higher workloads. Some excitation of SOL and TA still was required. However, HAM and RF were not excited at all and freewheeling occurred.

Smooth one-legged pedaling in the forward direction was found to be possible with the four groups, though the excitation levels among the groups had to be quite different (Fig. 5A). The EXT group was not excited, even during limb extension, but...
the FLEX and RF/TA groups had to be excited with more intensity. The FLEX group, which produces three times less energy than the EXT group in two-legged pedaling (Raasch et al. 1997), was required in one-legged pedaling to generate more power in the upstroke than the EXT group does in downstroke because the weight of the leg decelerates the crank in upstroke and accelerates the crank in downstroke. Because the weight of the limb opposes the initial part of the flexion-to-extension transition (Fig. 5A, diagram), the RF/TA group also must contribute more energy than the HAM/TS group in one-legged pedaling. With all four groups excited at the same (high) intensity, pedaling with one leg was feasible but it was very nonsmooth (nonsmoothness cost of 22 vs. 0.8 rpm for unequal excitation) and freewheeling occurred (Fig. 5B). With a lower intensity of excitation of the groups, pedaling through limb flexion was impossible (not shown).

**Backward pedaling**

Continuous backward pedaling was found to be impossible with the four groups excited at the same intensity and phasing as in forward pedaling, where phasing is relative to limb extension, flexion, and the extension/flexion transitions (Fig. 6A). The resulting freewheeling and reversals in crank direction at the limb transitions were due to the high deceleration of the crank caused by ipsilateral HAM and contralateral RF forces near 180°, and ipsilateral RF and contralateral HAM forces near 360°. This retardation became evident by analyzing

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**Fig. 4.** Optimal 4-group coordination pattern for minimizing metabolic energy consumption when pedaling forwards. ⊗, optimal pattern; ◦, nominal pattern (see Fig. 3).

**Fig. 5.** One-legged forward pedaling. A: muscle groups excited at different intensities but phased identically as in 2-legged pedaling (Fig. 2). Left: circular-bar width shows excitation level; HAM/TS group excited at 45%, somewhat higher than the nominal amount, FLEX and RF/TA groups maximally excited, and EXT group not excited. Right: crank angular velocities \(q_{\text{crank}}\) for 1- and 2-legged pedaling. B: muscle groups in 1-legged pedaling excited as in nominal 2-legged pedaling (i.e., phasing the same as in Fig. 2A and all groups excited at 77% of maximum). Wide region of freewheeling (◦ at top; see text) is associated with extreme variations in \(q_{\text{crank}}\) (compare — with - - -). Note that scales in A and B differ.

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**Fig. 6.** Backward pedaling with 2 legs. A, left: 4 muscle groups excited at the same intensity and phased according to limb extension and flexion and their transitions as in forward 2-legged pedaling (Fig. 2). Right: crank speed for backward pedaling (—) and forward pedaling (- - -). Positive speed indicates the crank is moving in the desired direction. Backward progressing crank (—) freewheels (◦) and slows at the 1st transition \((\sim 180°)\), and then cannot progress backward through the 2nd \((\sim 360°)\), which contrasts sharply with the steady progression in forward pedaling (- - -). B, left: all muscles in the 4 muscle groups still phased according to limb extension and flexion and their transitions, as in forward pedaling, except HAM and RF muscles are not excited. Right: crank still freewheels at the transitions, resulting in highly nonsmooth pedaling, but backward progression is possible. C, left: all muscles phased as in forward pedaling except HAM and RF muscles are phase reversed (i.e., excited at the opposite limb transition). All muscles excited at the same equal intensity as in forward pedaling (i.e., 27%). Right: freewheeling is absent and backward progression is smooth as in forward pedaling. Note the less-sensitive crank-speed scale in A.
the contributions of the HAM/TS group and the RF/TA group to the two propulsive components essential to cranking the limb through its transitions (i.e., through 180° and 360°), which are to accelerate the crank and to transfer energy from the limb inertia to the crank (Raasch et al. 1997). Continuous backward pedaling was, nevertheless, possible as long as HAM and RF muscles were not excited anywhere in the crank cycle and the other muscles were excited as in forward pedaling, although freewheeling occurred at transitions (Fig. 6B). In this case, TS and TA muscles were able to transfer to the crank the energy delivered previously to the limb inertia by the EXT and FLEX groups, respectively, as in forward pedaling (Raasch et al. 1997).

Very smooth backward pedaling was achievable with the groups excited at the same intensity, however, if the RF/TA-HAM/TS pair was subdivided into two pairs (RF-HAM pair and TA-TS pair; Fig. 6C). Importantly, the phasing of the HAMS and RF groups had to be reversed from that required in forward pedaling, relative to the limb transitions, so they could propel the crank through the limb transitions (cf. Fig. 6C with Fig. 2A near 180° and 360°). Decoupled from HAM and RF, the TS and TA groups were able to transfer energy from limb inertia to crank as in forward pedaling. With the RF and HAM groups now able to provide crank propulsion at the limb transitions rather than retardation, excitation of all six groups could be at the same intensity.

**Discussion**

Continuous, smooth, efficient pedaling in the forward direction at different cadences and workloads was found to be possible with just four muscle groups of coexcited muscles. The successful pattern is simpler than four independent controls because each group alternates with another (i.e., 2 pairs, with each pair consisting of 1 muscle group alternating with another). In fact, a control strategy that is constrained further to excite all muscles at the same intensity also suffices well. However, the excitation levels of the groups must be different to accomplish different pedaling goals, such as to pedal smoothly with one or two legs or to pedal with the highest energetic efficiency.

**Robust pedaling strategy: six muscle groups arranged into three pairs**

We believe that a strategy employing fewer than six muscle groups is not biomechanically adaptable to be considered a general pedaling strategy because pedaling forward and backward imposes different biomechanical requirements. Nevertheless, it is possible, at times, to turn the crank forward and backward by controlling less than six groups (e.g., 4 groups, Figs. 2A and 6B). In this case, smooth crank progression when pedaling in reverse is impossible because no four-group excitation pattern that smoothly pedals, say, forward can accelerate the crank backward at the limb transitions adequately (e.g., cf. Fig. 6B with Fig. 2). In fact, if the frictional load is sufficiently high, continuous progression in reverse is not possible at all, and the demand for six muscle groups to be controlled becomes even more evident.

Of course, pedaling with fewer than four groups is even less adaptable, not only with respect to pedaling direction but even in a given direction. For example, continuation of forward cranking is impossible when the biarticular thigh and the ankle muscles are combined with either the FLEX or the EXT group (Fig. 7A, left). The leg oscillates forward/backward at the limb extension/flexion transitions (Fig. 7A, right). Changing the phasing of the groups of the one pair, or the grouping of muscles, does not improve performance because the EXT and FLEX muscles then decelerate the crank during their relaxation. Also the improperly phased biarticular thigh and ankle muscles are then unable to provide propulsion at the limb transitions. Shortening the burst durations of the two groups of the one pair alleviates the otherwise high deceleration during limb extension and flexion, but freewheeling still occurs at the limb transitions (Fig. 7B). For smooth pedaling, the biarticular thigh and ankle muscles must be excited during the limb transitions (Raasch et al. 1997). Of course, any strategy that delivers sufficient energy to overcome the load and propel the limb will suffice to turn the crank, although not necessarily smoothly (e.g., the metabolically efficient use of EXT, SOL, and TA in the unconstrained optimization). If the inertia of the ergometer is very high (e.g., to emulate bicycle riding) (Fregly et al. 1996), such a strategy might even produce acceptable smoothness. Hard-coupling of the crank and flywheel would simplify further control of smooth pedaling because the inertia of the flywheel would assist the limb in coasting through transitions.

The ability to control six muscle groups to execute six
biomechanical functions is required, therefore, to be able to fulfill a variety of pedaling goals, including forward and backward pedaling. Four groups are insufficient because the phasing of the HAM and RF groups are directionally sensitive and the phasing of the TS and TA groups are not. Thus HAM control must be separated from TS control and RF from TA control. Nevertheless HAM and RF still can be paired because they still alternate with one another, and TS still can be paired with TA. Similar uncoupling of muscles is seen in posture, where the “ankle strategy” (HAM/T5 alternating with RF/TA) is in some situations replaced with a mixed strategy (Horak and Nashner 1986). The “coupling” of HAM/TS and RF/TA in the four-group control may be more accurately described as “coincidence” because the groups actually serve different biomechanical functions in pedaling.

The ankle muscles (TS-TA pair, particularly TS) must position the feet properly at the limb transitions to transfer energy from the limb to the crank. This transition redirects energy that would otherwise go toward accelerating the limb segments, prevents extreme ankle dorsiflexion and knee hyperextension at the end of limb extension, and avoids excessive ankle plantarflexion at the end of limb flexion (Raasch et al. 1996; Raasch et al. 1997). Indeed, other backward-pedaling simulations by us with TS-TA switched in phase do indeed hyperextend the knee. Thus the phasing of TS should be near the end of limb extension (i.e., following/overlapping activation of the EXT group), and TA near the end of flexion, irrespective of pedaling direction (Figs. 2A and 6C). The TS-TA pair therefore is associated closely with the EXT-FLEX pair with a phase delay between the pairs to properly configure the limb segments for energy transfer (cf. alternative strategies, see following text).

In contrast, HAM and RF act primarily to accelerate the crank when the leg is moving posteriorly (HAM) or anteriorly (RF), also regardless of pedaling direction. Their phasing, however, reverses with pedaling direction (Figs. 2A and 6C). Other simulations by us also support the decoupling of HAM-RF from TS-TA and the different biomechanical functions executed by these two pairs. For example, with the two pairs separated, maximum smoothness is obtained by exciting HAM-RF more than TS-TA because more crank power is desired at the transitions and HAM and RF can produce such power. On the other hand, maximum metabolic efficiency is obtained by exciting TS more because the ankle must be stabilized to ensure more complete transfer of the EXT-produced energy to the crank.

A strict association between each of the six functional muscle groups and a specific biomechanical function, as emphasized earlier for clarity, however, should be viewed cautiously because recent studies suggest that a muscle can contribute to more than one biomechanical function in pedaling (Neptune et al. 1997; Ting et al. 1999). For example, a backward-pedaling experimental study showed that the transition muscles HAM and RF change their phasing, as compared with forward pedaling (Ting et al. 1999). However, the change in RF phasing was much less than 180°, probably because RF contributes to limb extension as well as to the flexion-to-extension transition function. Nevertheless all these studies agree that six biomechanical functions must be performed to pedal smoothly. The association of a functional muscle group with a biomechanical function, initially proposed by Raasch et al. (1997), thus provides a foundation for interpreting pedaling EMG patterns.

Alternative ankle-control strategies

Analysis of the differences between simulated pedaling with the four muscle groups and the kinetics and EMGs recorded from pedaling subjects (Fig. 2B) suggests that a variety of ankle strategies are possible. EMG amplitudes are unequal from one another, probably due to their dependence on the specific pedaling task (e.g., pedaling both smoothly and efficiently; cf. Figs. 3 and 4). The earlier onset of TA and SOL in pedaling subjects is probably due to subjects employing a different ankle strategy than assumed in the simulation. Simulations show that some latitude is possible in controlling the ankle (i.e., TA and SOL) as long as the essential biomechanical requirement of transfer of energy from the hip and knee extensors to the crank is accomplished. SOL and TA may be excited earlier because of their participation in the execution of the EXT and FLEX biomechanical functions (i.e., extension/flexion of the limb). In this case, SOL and TA still stiffen the ankle to facilitate energy transfer from the limb to the crank, but the stiffening is earlier. Consequently less kinetic energy is stored temporarily in the limb segments. Pedal kinematics then more closely match the subjects’ (e.g., peaks in pedal angles are reduced) and ankle motion is reduced. This explanation is compatible with the suggested secondary contribution of TA to flex the limb in pedaling (Ting et al. 1999) and the suggested contribution of SOL to extend the limb as well as plantarflex the foot (Neptune et al. 1997). Another feasible ankle strategy is to maintain the foot near-horizontal throughout the cycle (a strategy more “comfortable” for many subjects). In this case, SOL and TA must be excited slightly through much of down- or up-stroke, even though this does not contribute significantly to crank acceleration (and hence is not selected by an optimization that does not consider comfort). Still other strategies are possible; for example, “locking” the ankle in a plantarflexed position for much of the cycle with prolonged TS excitation (Raasch 1996). Such a strategy effectively removes the ankle degree of freedom and prevents knee hyperextension. However, this ankle strategy requires more metabolic energy than the default strategy, and the resulting kinematics may be undesirable for subjects.

Phase control of motor output

Timing of the excitation of the muscle groups within the pedaling cycle could be regulated by afferent feedback from the limbs as in locomoting animals (Pearson 1993; Rossignol et al. 1988). An estimate of the position of the feet relative to the hips through neural processing of afferent information could be the trigger signal for limb extension and flexion, as in animal locomotion (Andersson and Grillner 1983; Grillner and Rossignol 1978). Phasing of the TS-TA pair could be time delayed from EXT-FLEX phasing to assure appropriate transfer of energy from the limb inertia to the crank. Although a continuous estimate of feet location also could be used to precisely time (i.e., phase-control) the excitation of all six groups within the cycle, motion-dependent cues (e.g., anterior/posterior motion of the ankles) also may participate. For example, if RF was to be excited when the ankle is moving anteriorly, and HAM when moving posteriorly, then the HAM-RF pair would be phased properly in both forward and backward pedaling. If the phasing of the biarticular thigh muscles is set primarily by
motion-dependent feedback, similar to the ‘‘mutable synergies’’ postulated by Smith (1987) in the restructuring of the cat locomotor pattern, simple rule-based logic networks acting on sensory information might be sufficient to implement the required phase control (Cruse et al. 1995a,b). Such control of locomotion is being employed in the development of Functional Electrical Stimulation controllers to restore gait in paraplegics (Popovic 1991, 1993).

**Gain control of motor output**

Pedaling at a faster cadence or a higher workload can be achieved by increasing the excitation of the muscle groups equally. This regulation of cadence and power output could be accomplished by a common gain control of the excitations of the muscle groups. Common gain control could be effected by neural control and neuromodulator concepts derived from animal locomotion studies (Grillner 1981, 1988; Pearson 1993; Rossignol et al. 1988). For example, a descending tonic drive from supraspinal structures onto pattern generator elements could set the common scaling factor for excitation of the muscle groups compatible with the desired limb power output (equivalent to a certain cadence with a specific energy output from the limb per cycle), similar to the setting achieved by descending pathways from brain stem locomotor regions (Grillner 1988; Shik et al. 1996).

Regulation of the intensity of motor output could be accomplished by afferent feedback. Neural processing of load-sensing feedback from the limb in pedaling (Raasch 1996) or walking (Duyssens and Loeb 1980; Duyssens and Pearson 1976, 1980; Pearson et al. 1992), should be especially effective (Raasch et al. 1997).

**Relative excitation levels of the muscle groups**

Some pedaling tasks require the excitation levels of the muscle groups to be different, such as to pedal with one leg or to pedal with ultrasmoothness or the highest energetic efficiency. Processing of afferent feedback to ensure that the specific goals of the pedaling task are fulfilled could be attained through high-level control of parameters utilized by a lower-level controller (Loeb et al. 1990; Prochazka 1989). In this scheme, a specific pedaling task would be accomplished by the setting of parameters, or ‘‘schedules’’ (Prochazka 1989), which may be part of the initialization of the pedaling motor program. This could allow for a more complex ‘‘recruitment scheme’’ for muscles within a group, as conditions require, as seen in the selective activation of individual extensor muscles with increased load when muscles were allowed to be excited independently (Raasch 1996). After initial parameter selection by the high-level controller, pedaling could proceed by activating the low-level controller. Feedback would be used by the high-level controller only to check periodically (e.g., once per half-cycle) the appropriateness of the parameter set (e.g., the phasing and excitation-level parameters of each muscle group). In conjunction with the parameter set, feedback would be employed by the low-level controller to assure continuous task execution in the presence of ‘‘reasonable’’ environmental (and internal) uncertainties; e.g., muscle and joint receptors could be used to modulate TS-TA to prevent excessive ankle motion and fine-tune the control of the pedal trajectory.

**Locomotor strategies in animals and humans may be similar**

The locomotor features outlined in the preceding text based on pedaling, with muscles organized into alternating functional groups and phase- and amplitude-controlled (perhaps through high- and low-level neural controllers), have features common to animal locomotion. First, spinal neuronal elements exciting motor pools alternately through (perhaps) other interneurons have long been the basis of locomotor concepts (Grillner 1975), and now their cellular, molecular, and pharmacological properties are being elucidated in even vertebrates (Grillner 1988; Rossignol and Dubuc 1994). Second, phase-control of these elements through neural processing of peripheral proprioceptive information is critical to pattern generator execution of locomotion (Pearson 1993; Rossignol et al. 1988). For example, load-bearing feedback in animal locomotion is important to flexor initiation and excitation of the extensors (Pearson and Duyssens 1976), and to the relative excitation of flexors to extensors (Smith and Carlson-Kuhta 1995). In pedaling, because cranking force (and the reaction force felt on the foot) is primarily a function of the contributing muscle forces (Kautz and Hull 1993), force feedback could be used to balance the excitation between the EXT and FLEX groups (e.g., as required to achieve 1-legged pedaling, Fig. 5). Also, the position of the limb relative to the hip is critical to phase selection in cat locomotion (Andersson and Grillner 1983; Grillner and Rossignol 1978) and could be in human pedaling as well (see preceding text).

The features used by humans to provide propulsion to walk and pedal also may be similar (see introduction). For example, the switch in phasing of the thigh bifunctional muscles (e.g., HAM and RF) with walking direction (Thorstensson 1986) and to anterior/posterior postural balance disturbances (Nashner and McCollum 1985) is similar to the switch occurring in HAM and RF in pedaling. We believe, therefore, that humans pedal by using some of the sensorimotor control mechanisms employed to walk (and stand).

**Conclusion**

When muscles are assigned into groups, our simulations show that six groups are the minimal set to pedal in different directions under a variety of conditions. Phasing of four groups (uniarticular hip and knee extensors in alternation with hip and knee flexors; ankle plantarflexors in alternation with dorsiflexors) do not change with direction. The biarticular thigh muscles (anterior alternating with posterior muscles) do change with direction (e.g., rectus femoris is excited during the transition from flexion to extension in forward pedaling and during the opposite transition from extension to flexion in backward pedaling). Different cadences and limb power output can be achieved by controlling the overall excitatory drive to the pattern generating elements, and different pedaling goals (e.g., 1- versus 2-legged pedaling) can be achieved by controlling the relative excitation levels among the muscle groups. We suggest that these six muscle groups form a basic strategy for pedaling propulsion and also may be a subset of the elements of a general strategy for human locomotor propulsion. We believe that pedaling affords a rich milieu for performing not only detailed theoretical studies, such as those here, but also for conducting controlled locomotor experiments in healthy and
neurologically impaired subjects (Brooke et al. 1987, 1992;
Pierson-Carey et al. 1997; Ting et al. 1998, 1999), which together may reveal motor control mechanisms of human loco-

We thank D. Brown and L. Ting for very helpful comments on an earlier version of the manuscript, S. Kautz for insightful suggestions for improving the different drafts of the manuscript, and D. Denney for assistance with figure preparation. Special thanks to R. Neptune for providing us with experimental pedaling data (Neptune et al. 1997).

The work was supported by National Institute of Neurological Disorders and Stroke Grant NS-17662 and the Rehabilitation R&D Service of the Department of Veterans Affairs (VA).

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Received 26 May 1998; accepted in final form 22 March 1999.

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