

Phase Reversal of Biomechanical Functions and Muscle Activity in Backward Pedaling

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Ting, Lena H., Steven A. Kautz, David A. Brown, and Felix E. Zajac. Phase reversal of biomechanical functions and muscle activity in backward pedaling. *J. Neurophysiol.* 81: 544–551, 1999. Computer simulations of pedaling have shown that a wide range of pedaling tasks can be performed if each limb has the capability of executing six biomechanical functions, which are arranged into three pairs of alternating antagonistic functions. An Ext/Flex pair accelerates the limb into extension or flexion, a Plant/Dorsi pair accelerates the foot into plantarflexion or dorsiflexion, and an Ant/Post pair accelerates the foot anteriorly or posteriorly relative to the pelvis. Because each biomechanical function (i.e., Ext, Flex, Plant, Dorsi, Ant, or Post) contributes to crank propulsion during a specific region in the cycle, phasing of a muscle is hypothesized to be a consequence of its ability to contribute to one or more of the biomechanical functions. Analysis of electromyogram (EMG) patterns has shown that this biomechanical framework assists in the interpretation of muscle activity in healthy and hemiparetic subjects during forward pedaling. Simulations show that backward pedaling can be produced with a phase shift of 180° in the Ant/Post pair. No phase shifts in the Ext/Flex and Plant/Dorsi pairs are then necessary. To further test whether this simple yet biomechanically viable strategy may be used by the nervous system, EMGs from 7 muscles in 16 subjects were measured during backward as well as forward pedaling. As predicted, phasing in vastus medialis (VM), tibialis anterior (TA), medial gastrocnemius (MG), and soleus (SL) were unaffected by pedaling direction, with VM and SL contributing to Ext, MG to Plant, and TA to Dorsi. In contrast, phasing in biceps femoris (BF) and semimembranosus (SM) were affected by pedaling direction, as predicted, compatible with their contribution to the directionally sensitive Post function. Phasing of rectus femoris (RF) was also affected by pedaling direction; however, its ability to contribute to the directionally sensitive Ant function may only be expressed in forward pedaling. RF also contributed significantly to the directionally insensitive Ext function in both forward and backward pedaling. Other muscles also appear to have contributed to more than one function, which was especially evident in backward pedaling (i.e., BF, SM, MG, and TA to Flex). We conclude that the phasing of only the Ant and Post biomechanical functions are directionally sensitive. Further, we suggest that task-dependent modulation of the expression of the functions in the motor output provides this biomechanics-based neural control scheme with the capability to execute a variety of lower limb tasks, including walking.

INTRODUCTION

Backward locomotion provides an opportunity to test the adaptability of pattern generators in the control of locomotion

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(e.g., Ashley-Ross and Lauder 1997; Duysens et al. 1996), although neural control mechanisms are best elucidated with an understanding of the biomechanics of forward and backward locomotion (Zernicke and Smith 1996). Grillner (1981) suggested that backward walking in the cat could be produced by a phase shift in activation of unit burst generators controlling flexion and extension of knee and hip muscles. Studies of backward walking in humans and cats have shown, however, that the reconfiguration of the motor pattern proposed by Grillner (1981) has limitations (Buford and Smith 1990; Pratt et al. 1996; Vilensky et al. 1987). Further, although joint power (Winter et al. 1989) and limb kinematics (Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989) are essentially reversed in time during backward walking, electromyogram (EMG) activity is not reversed in all muscles (Duysens et al. 1996; Thorstensson 1986; Winter et al. 1989). However, it is unknown whether a strict reversal of muscle activity patterns or a phase shift in activation of knee and hip muscles (Grillner 1981) is biomechanically sufficient to produce backward walking. Thus whether differences observed experimentally arise from neural adaptations to fulfill task biomechanics or from fundamental differences underlying neurophysiological control cannot be ascertained.

Computer simulations can be used to test whether a motor activity pattern can generate backward locomotion. Simulations of walking are, however, difficult to achieve because of the instability associated with bipedal balance and weightbearing (Yamaguchi and Zajac 1990). These instabilities are absent in pedaling, thus providing a rhythmic locomotor task that can be simulated and analyzed in isolation of the postural task (Kautz and Brown 1998; Neptune et al. 1997; Raasch et al. 1997). Pedaling is also an ideal experimental locomotor paradigm because cadence, speed, limb phasing, limb excursion, and workload can be kept similar. Further, because many muscle coordination patterns can successfully produce forward pedaling (Raasch 1996), task biomechanics do not overly constrain the set of feasible control strategies. Thus insight into neural control of locomotion is possible.

Simulations of pedaling offer insight into muscle coordination (Fregly and Zajac 1996; Raasch et al. 1997) by revealing muscle contributions to joint torques and accelerations not possible from kinematic, kinetic, and EMG observations alone. For example, the hamstrings (HAMS) do not accelerate the knee into flexion to prevent knee hyperextension as the limb approaches full extension (cf. Gregor et al. 1985; van Ingen Schenau 1990), but rather the knee is accelerated into exten-

sion and the crank is accelerated as well (Andrews 1987; Carlsoo and Molbech 1966; Raasch et al. 1997). The reason the knee is not accelerated into flexion is that the hip extensor torque produced by HAMS acts to accelerate the knee, as well as the hip, into extension. Although the knee flexor torque produced by HAMS does indeed act to accelerate the knee into flexion, the effect of the hip extensor torque dominates. In fact, soleus (SL) is the muscle that prevents knee hyperextension in pedaling (Raasch et al. 1997). Muscles (or joint torques) can accelerate joints or body segments to which they do not attach or span because of joint reaction forces arising from the multijoint dynamical properties of the body, which are task and body-position dependent (Zajac and Gordon 1989). Such insight can be gained from forward simulations, which show the spatiotemporal contributions of joint torques (or muscle forces) to task execution, rather than from calculation of joint torques from external measurements, which are incapable of showing directly such contributions. Specifically, knowledge of pedaling biomechanics revealed through simulations was critical to the elucidation of the basic biomechanical functions in pedaling (Raasch et al. 1997).

Simulations capable of reproducing kinematics, kinetics, and muscle excitations in maximum-speed startup forward pedaling showed that muscles must execute six biomechanical functions (Raasch et al. 1997). The functions are performed in different regions of the crank cycle and can be organized into three pairs of alternating antagonistic functions to form a basis for a control strategy capable of producing a myriad of pedaling tasks (Fig. 1) (Raasch 1996; Raasch et al. 1997). Ting (1998) reformulated the six functions to be applicable to walking as well as pedaling (Fig. 1B). The Ext-Flex biomechanical function pair is defined by its contribution to the acceleration of the foot (or foot contact point with the environment), either away from (Ext) or toward the pelvis (Flex). Thus a muscle, which acts to accelerate the foot away from the pelvis, even if the leg is flexing, contributes to the Ext function (e.g., a muscle performing an eccentric contraction whose force acts to decelerate ongoing leg flexion). The Ant-Post pair is defined by its contribution to the acceleration of the foot with respect to the pelvis in the anterior (Ant) and posterior (Post) directions, respectively (Fig. 1B), orthogonal to that produced by the Ext-Flex functions. The Plant-Dorsi pair is defined by its contribution to an acceleration tending to either plantarflex (Plant) or dorsiflex (Dorsi) the foot.

This theoretical framework of biomechanical functions was used to analyze kinematic, kinetic, and EMG data observed in forward pedaling in healthy and neurological impaired individuals. Some muscles in healthy adult subjects pedaling at different cadences were found to contribute to one function, such as vastus medialis to Ext, gastrocnemius to Plant, hamstrings to Post, and tibialis anterior to Dorsi. Other muscles were found to contribute to two functions, such as rectus femoris to Ant and Ext and SL to Ext and Plant (Neptune et al. 1997). Analysis of muscle activity of pedaling hemiparetic individuals compared with healthy age-matched controls (elderly adults) showed that impaired ability to produce work and propel the crank is related to prolonged activity in muscles contributing to Ext function and to improper phasing in muscles contributing to Ant and Post functions (Kautz and Brown 1998).

On the basis of pedaling simulations (Raasch 1996), phasing

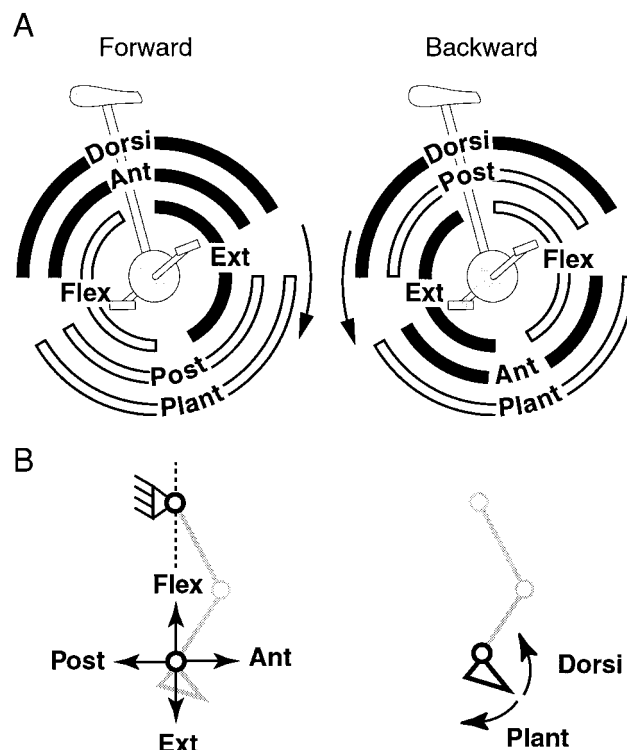


FIG. 1. Biomechanical functions derived from simulations (Raasch 1996; Raasch et al. 1997) capable of producing a variety of forward and backward pedaling tasks. *A*: phasing of the 6 biomechanical functions in forward and backward pedaling. The functions are arranged into 3 pairs (Ext-Flex, Dorsi-Plant, and Ant-Post), with each pair consisting of 2 antagonistic functions (e.g., Ext function and Flex function). Backward pedaling can be produced with a phase shift of 180° in the Ant-Post pair. *B*: Ext-Flex pair is defined by its contribution to the acceleration of the foot (or foot contact point with the environment), either away from the pelvis (Ext) or toward the pelvis (Flex); Ant-Post pair by its contribution to the acceleration of the foot with respect to the pelvis in the anterior (Ant) and posterior (Post) directions, orthogonal to that produced by the Ext-Flex pair; and Plant-Dorsi pair by its contribution to an acceleration tending to either plantarflex (Plant) or dorsiflex (Dorsi) the foot.

of four of the biomechanical functions (Ext, Flex, Dorsi, and Plant) or muscles contributing to the execution of the functions is proposed to be pedaling-direction invariant with respect to limb extension and flexion (Fig. 1A). Phasing of the other two functions (Ant and Post) are proposed to reverse in backward pedaling because they are related to anterior or posterior motion of the limb, which occur at the opposite limb extension/flexion transitions in backward pedaling. This study was to test whether a simple biomechanics-based control scheme of alternating muscle function pairs is sufficient to explain EMG phase shifts in backward pedaling. Because only a phase reversal of Ant and Post functions is theoretically sufficient to satisfy the biomechanical requirements of backward pedaling, only rectus femoris (RF) and HAMS were hypothesized to change phasing (cf. vastus medialis, gastrocnemius, tibialis anterior, and SL).

METHODS

Experimental setup

Sixteen healthy subjects [8 male, 8 female; age = 24 ± 7 (mean \pm SD) years; height = 1.74 ± 0.10 m; weight = 70 ± 9 kg] participated in the study. Experienced cyclists who had ridden >50 miles per week were excluded. This study was approved by the Institutional Review

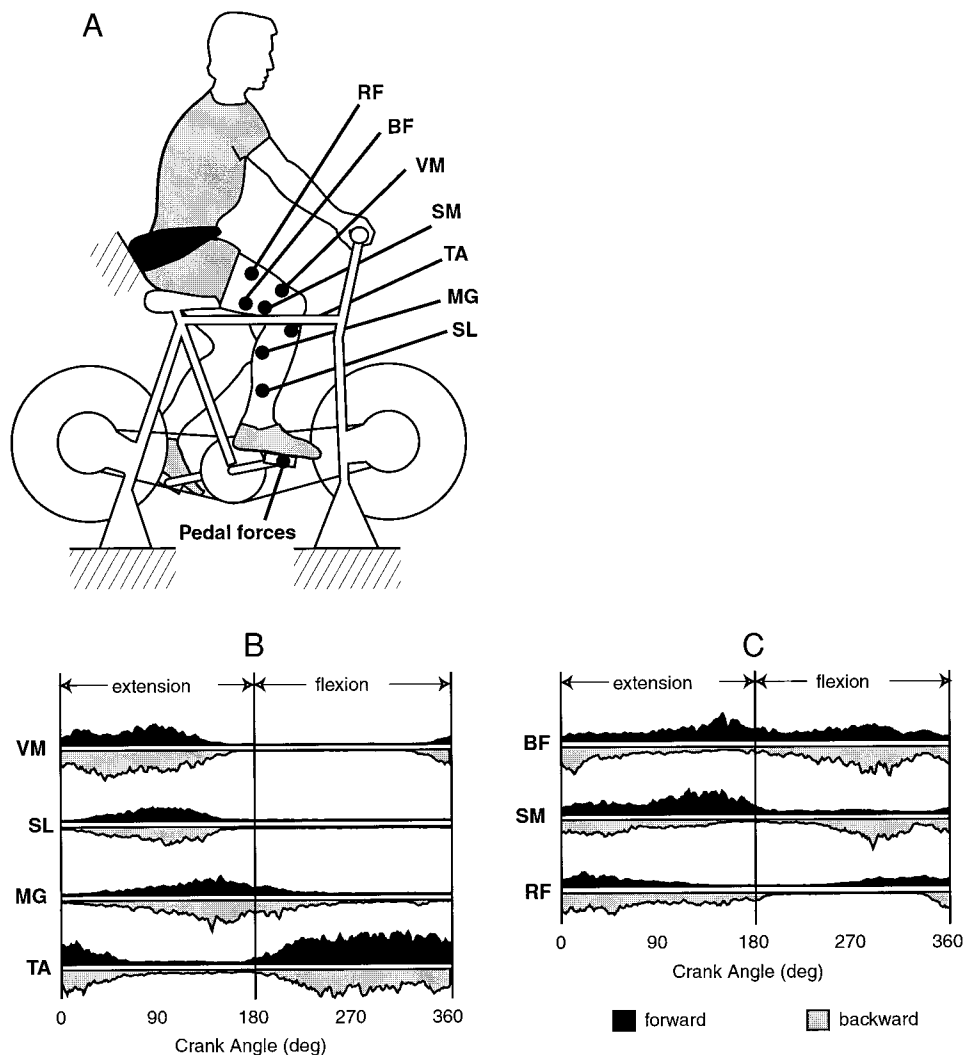


FIG. 2. Experimental setup and sample electromyograms (EMGs). A: subjects pedaled a bicycle ergometer with a chain attached to 1 of the 2 flywheels, allowing a constant workload to be applied in forward and backward pedaling. Pedal forces, crank angle, pedal angles, and 7 EMGs bilaterally were collected. Subjects used handlebars to maintain a nearly upright posture. A restraining belt at the hip minimized pelvic motion. B and C: representative EMGs from 1 subject in forward and backward pedaling. Vastus medialis (VM), soleus (SL), medial gastrocnemius (MG), and tibialis anterior (TA) maintained the same phasing in forward and backward pedaling B: biceps femoris (BF), semimembranosus (SM), and rectus femoris (RF) exhibited different phasing (C).

Board (Medical Committee for the Protection of Human Subjects in Research) at Stanford University. Each subject signed a consent form before participation.

Subjects pedaled a bicycle ergometer, modified to provide the same frictional workload (120 J/cycle) in both the forward and backward directions (Fig. 2A). Subjects were seated during all trials, with a restraining belt to minimize pelvic motion. Subjects grasped handlebars that allowed them to sit upright with a forward lean of about 10° from the vertical, consistent with trunk angles typically encountered during walking (Pozzo et al. 1990). Cleated cycling shoes provided a rigid connection between the feet and the pedals.

The force at each pedal spindle was measured with a pedal dynamometer (Newmiller et al. 1988). Optical encoders measured crank and pedal angles. Surface EMGs were collected bilaterally from vastus medialis (VM), RF, biceps femoris (BF), semimembranosus (SM), tibialis anterior (TA), medial gastrocnemius (MG), and SL. All data were sampled at 1,000 Hz (similar to those of Ting et al. 1998).

Practice protocol

Subjects were trained so that they could maintain a constant cadence of 60 rpm without feedback. First, subjects pedaled forward in two 60-s trials, using a metronome for the first 30 and 20 s, respectively. Subjects then pedaled backward in five 60-s trials, using a metronome for the first 40, 30, 20, 10, and 10 s of each trial, respectively. Subjects were given ≥ 1 min rest between each trial.

By the end of the practice session most subjects were able to pedal smoothly and consistently, maintaining a constant cadence between 55 and 65 rpm. A few subjects did not perform consistently and were given additional practice time. Smoothness was determined by the absence of freewheeling, a decoupling of the crank from the flywheel load that occurs when the crank decelerates relative to the flywheel (Fregly 1993; Raasch 1996).

Experimental protocol

Data were collected in four 40-s trials, two forward and two backward pedaling trials, presented in random order. Subjects used a metronome in the first 10 s, and data were collected in the last 15 s of each trial. Subjects were instructed to maintain a constant cadence and to pedal "smoothly and consistently."

Kinematic and kinetic data processing

Pedal force, crank angle, and pedal angle were downsampled to 200 Hz and low-pass filtered (10 Hz, zero-lag Butterworth filter). For each pedal, crank torque, which is the component of the force that accelerates the crank multiplied by crank arm length, was calculated from the pedal force and the pedal and crank angles. Kinematic variables were referenced to crank angle, with a reflected coordinate system for backward pedaling (Fig. 3A). By defining 0° as the position of the crank parallel to the seatpost when the leg is most flexed (pedal closest

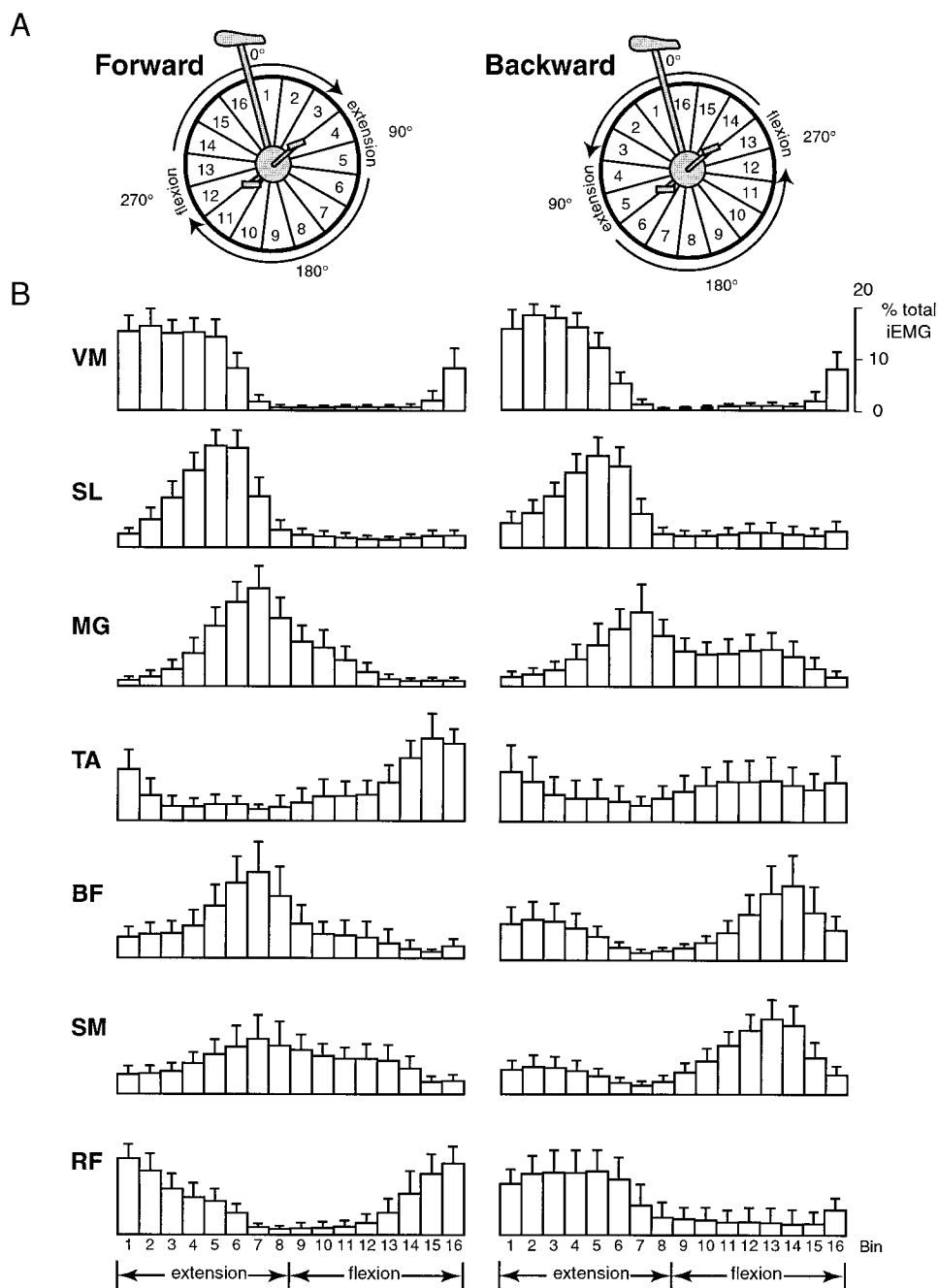


FIG. 3. Coordinate systems, phase intervals, and mean iEMGs. *A*: coordinate system and crank phase intervals used in analysis of forward and backward pedaling. The coordinate system is reflected about the seat tube in backward pedaling. In both pedaling directions, a crank angle of 0° occurs when the crank is aligned with the seatpost at maximum limb flexion. Crank angles increase in the direction of motion (i.e., $0-180^\circ$ corresponds to the extension phase and $180-360^\circ$ to the flexion phase). The crank cycle was divided into 16 phase intervals of 22.5° each (i.e., crank phase intervals of 1–8 refer to extension and 9–16 to flexion). EMGs were integrated over each of the 16 phase intervals in forward and backward pedaling. *B*: mean (SD) of normalized iEMGs for forward and backward pedaling in each of the 16 crank phase intervals averaged over all subjects. iEMG in each of the 16 intervals was normalized by the total iEMG. iEMG distributions were generally consistent across subjects. VM, SL, MG, and TA displayed no change in phasing during backward pedaling. BF, SM, and RF exhibited significant changes in phasing. In backward pedaling, secondary regions of activity may exist (e.g., MG during flexion phase).

to the pelvis) and defining positive crank angle in the direction of motion in both forward and backward pedaling, crank angles between 0 and 180° always correspond to limb extension (pedal moving away from the pelvis) and crank angles between 180 and 360° to limb flexion (pedal moving toward the pelvis). Data from each trial were ensemble averaged over 10 complete crank revolutions (~ 10 s).

To compare forward and backward crank torque generation, the amount of work done by each leg was calculated during limb extension and flexion. The work done in any region of the cycle is proportional to the average crank torque during that phase. The work done during extension was found by integrating the crank torque over 0 and 180° and work during limb flexion by integrating over 180 and 360° . Total workload was found by integrating the crank torque from both legs over the entire crank cycle ($0-360^\circ$). Work values were compared with two-way analysis of variance (ANOVA) with subject and pedaling direction as factors.

EMG data processing

To characterize the EMG profiles of each muscle, integrated EMG (iEMG) was calculated in 16 crank phase intervals of 22.5° over the entire crank cycle (Fig. 3A). Intervals 1–8 correspond to limb extension, and 9–16 to limb flexion. Total iEMG activity was found by summing the iEMG activity over the entire crank cycle (i.e., 16 intervals). Sixteen intervals were found to be adequate to represent changes in EMG yet sparse enough to allow for meaningful comparisons. For each trial, the iEMG profiles were ensemble averaged over 10 crank cycles. For each muscle and subject, an average iEMG profile for each pedaling direction was found by averaging each of the two forward or two backward pedaling trials. Left and right legs were analyzed independently.

To compare the phasing of iEMG profiles in forward and backward pedaling without regard to iEMG amplitude, each iEMG profile was

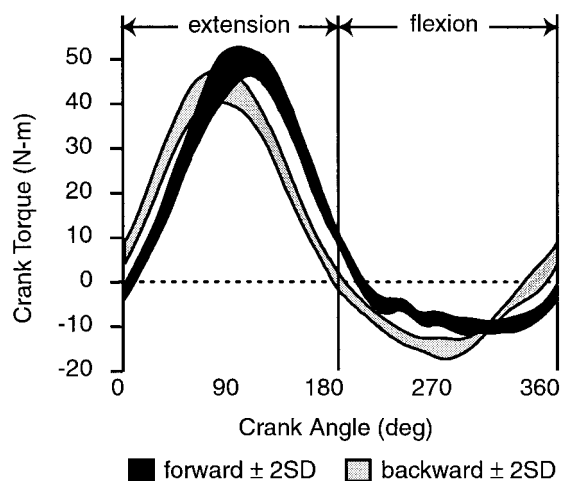


FIG. 4. Crank torque generated by 1 leg during forward and backward pedaling. Shaded area represents the mean \pm SD of the crank torque generated by 1 subject. The torque trajectory shapes were similar in forward and backward pedaling, with positive crank torque generated during leg extension and negative torque generated during leg flexion.

normalized by the total iEMG value for that trial. The Pearson product-moment correlation (r) was then calculated at all 16 possible phase shifts between the forward and backward pedaling profile for each muscle and subject

$$r_T = \sum_{i=1}^{16} \frac{(f_i - \bar{f})(b_i - \bar{b})}{(n-1)s_f s_b} \quad (1)$$

where f_i represents the i th element of the 16-element normalized iEMG vector of a particular muscle in forward pedaling and b_i in backward pedaling. The subscript T represents the relative phase shift tested, with a positive shift indicating a phase delay in backward compared with forward pedaling and a negative shift a phase advance. \bar{f} and \bar{b} represent the mean of the vectors f and b , respectively, and s_f and s_b represent the standard deviation of the vectors.

The phase shift, T_{\max} , corresponding with the maximum correlation coefficient, r_{\max} , identifies the phase relation at which the forward and backward iEMG profiles are most similar. The coefficient of determination, r_{\max}^2 , represents the percentage of signal energy distribution common to both signals at the phase shift T_{\max} , i.e., the degree to which the backward pedaling iEMG profile could be explained by the forward iEMG profile shifted by T_{\max} . The phase shifts found in this manner can be used to determine whether muscle timing in backward and forward pedaling are similar or different. Only shifts of greater than one bin, or 22.5° , are meaningful.

To compare overall iEMG amplitude between forward and backward pedaling, total iEMG was calculated for each muscle (left and right) in each subject. The values were analyzed with an ANOVA with subject and side (left or right, nested within subject) as blocking factors and pedaling direction as a factor.

RESULTS

Subjects successfully pedaled without freewheeling at the same cadence and against the same workload in both forward and backward pedaling. The average cadences for forward and backward pedaling were not significantly different (62 ± 1 rpm, and 61 ± 2 rpm, respectively, $P > 0.05$). No significant difference in total workload over the cycle was found between forward and backward pedaling (forward: 130 ± 14 J, backward: 124 ± 6 J; $P > 0.05$).

The shape and magnitude of the crank torque trajectories from one leg in forward and backward pedaling were also similar, exhibiting a large peak in crank torque during limb extension, and negative torque generation during limb flexion (e.g., Fig. 4). Furthermore, no difference in the amount of work done during backward and forward pedaling was found during either limb extension (forward: 73 ± 10 J, backward: 71 ± 9 J; $P > 0.05$) or limb flexion (forward: -8 ± 5 J, backward: -9 ± 9 J; $P > 0.05$).

EMG phase shifts

During both forward and backward pedaling, each muscle exhibited a major burst of EMG activity once per cycle (e.g., Fig. 2, B and C). Forward pedaling EMGs were similar to those previously reported (e.g., Ryan and Gregor 1992). Backward pedaling EMGs have not been previously reported. In each muscle, the phasing of the burst of activity was consistent across all subjects in both directions (Fig. 3B). Of the seven muscles investigated, four exhibited the same phasing in forward and backward pedaling (e.g., Fig. 2B). Three exhibited altered phasing (e.g., Fig. 2C).

Phasing of activity in VM, SL, MG, and TA was the same in forward and backward pedaling, as the mean phase shift T_{\max} was less than one bin (i.e., $<22.5^\circ$, Table 1). VM and SL were active only during limb extension (Fig. 3B). TA was active primarily at the flexion-to-extension transition and MG at the opposite transition (Fig. 3B).

Phasing of activity in BF, SM, and RF was different in backward and forward pedaling (Table 1). BF activity in backward pedaling was delayed $166 \pm 74^\circ$. In forward pedaling peak BF activity occurred just before the extension-to-flexion transition and in backward pedaling just before the opposite (flexion-to-extension) transition (Fig. 3B). SM activity in backward pedaling was delayed $107 \pm 57^\circ$. In 22 of 32 SM EMG comparisons (one EMG comparison/leg in 16 subjects), the average shift was $139 \pm 32^\circ$, closer to the shift found for BF (cf. SM with BF, Fig. 3B). In the other 10 SM EMG comparisons, peak SM activity occurred at midflexion during both forward and backward pedaling (compared with only 2 records in the BF), resulting in an average shift of just $36 \pm 39^\circ$. RF was active during the flexion-to-extension transition and into limb extension in forward pedaling, but in backward pedaling the burst, which occurred during limb extension, was shorter (Fig. 3B). In backward pedaling, RF was delayed by $51 \pm 38^\circ$ (Table 1).

TABLE 1. Comparison between forward and backward pedaling integrated electromyogram (iEMG)

| Muscle | Shift, deg | r_{\max}^2 | Change in Total iEMG |
|--------|----------------|-------------------|----------------------|
| VM | (-2 ± 11) | $0.90 \pm 0.06^*$ | NS |
| SL | (-7 ± 11) | $0.85 \pm 0.16^*$ | $-10\% \ddagger$ |
| MG | $(+16 \pm 34)$ | $0.64 \pm 0.21^*$ | $-11\% \ddagger$ |
| TA | (0 ± 54) | $0.62 \pm 0.16^*$ | NS |
| BF | $+166 \pm 74$ | $0.66 \pm 0.17^*$ | $-32\%^*$ |
| SM | $+107 \pm 57$ | $0.67 \pm 0.20^*$ | NS |
| RF | $+51 \pm 38$ | $0.77 \pm 0.10^*$ | NS |

Values are means \pm SD. VM, vastus medialis; SL, soleus; MG, medial gastrocnemius; TA, tibialis anterior; BF, biceps femoris; SM, semimembranosus; RF, rectus femoris. $*P < 0.01$. $\ddagger P < 0.05$.

EMG correlation coefficients

In each muscle, the EMG signal energy common in forward and backward pedaling was highly significant ($P < 0.01$, Table 1). In VM and SL, the correlation coefficient of determination, r_{\max}^2 , was very high (0.90 and 0.85, respectively), indicating that the signal energy distribution was essentially identical between forward and backward pedaling. Because the VM and SL have very distinct bursts in forward pedaling, the same pattern characterizes their activity in backward pedaling. In the other muscles (TA, MG, BF, SM, and RF), however, the signal energy distribution common in forward and backward pedaling was less ($0.62 \leq r_{\max}^2 \leq 0.77$). In the worst case, TA had r_{\max}^2 of 0.62, indicating that 38% of the signal energy distribution was unaccounted for by a phase shift. The unaccounted signal energy probably results from these muscles having more than one region of activity in the crank cycle with, usually, unequal activity in the regions. For example, it can be seen from the ensemble iEMGs of MG in backward pedaling (Fig. 3B) that, although the primary activity occurs at about the same crank phase as in forward pedaling, significant signal energy also exists throughout limb flexion. In RF, the unaccounted signal energy probably results from the unequal burst durations in the two pedaling directions.

EMG amplitude

The total iEMG amplitude in BF decreased by 32% during backward pedaling ($P < 0.01$, Table 1). However, the level of BF activity in backward pedaling compared with forward pedaling varied greatly across subjects. Some had very little BF activity during backward pedaling (8/32 had $<50\%$ total energy compared with forward pedaling), whereas a few demonstrated equivalent or higher total iEMG levels in backward pedaling (10/32 had $>90\%$ total energy compared with forward pedaling).

The only other muscles to exhibit a change in total iEMG in backward pedaling were SL (-10% , $P < 0.05$) and MG (-11% , $P < 0.01$; Table 1). VM, TA, RF, and SM exhibited no change in total iEMG.

DISCUSSION

As hypothesized, we found phasing changes in pedaling to occur in only those muscles (BF, SM, and RF) contributing to the execution of the Ant and Post biomechanical functions (Neptune et al. 1997; Raasch et al. 1997). Our contention that the phasing of only the Ant and Post biomechanical functions are directionally sensitive is therefore supported. However, these biarticular muscles did not necessarily contribute to the same function(s) in forward and backward pedaling. Also, other muscles were found to contribute somewhat to other functions in backward pedaling, which were not expressed in forward pedaling. It is suggested that the ability of a muscle to contribute to more than one function, with the expression of each in the motor output under neural modulation, gives the biomechanics-based neural control scheme flexibility and thus the capability to execute a variety of lower limb tasks, including walking.

EMGs compared with predicted muscle excitations based on biomechanical functions

Phasing of some muscles (VM, SL, MG, and TA) were unaffected by pedaling direction, consistent with their role being to contribute to the execution of a directionally insensitive biomechanical function (i.e., VM and SL to Ext; MG to Plant; TA to Dorsi; see Fig. 1A). Data from simulations and other experiments on forward pedaling are consistent with these muscles contributing to these functions (Neptune et al. 1997; Raasch 1996). However, at higher loads or cadences, at least in forward pedaling, SL contributes significantly also to Plant function (Neptune et al. 1997; Raasch et al. 1997; Ryan and Gregor 1992).

Phasing of the other muscles (BF, SM, and RF) were affected by pedaling direction, consistent with their role being to contribute to the two directionally sensitive biomechanical functions (i.e., BF and SM to Post; RF to Ant). The largest changes in phasing were found in BF and SM, probably because these muscles contribute mostly to Post, although a contribution to Flex probably occurs as well (Fig. 3). Indeed, a SM burst during limb flexion is evident at high cadences (Neptune et al. 1997). The smaller but still notable change in phasing in RF is due to its shorter burst in backward pedaling, which may be due to RF only contributing to Ext rather than to both Ext and Ant (Fig. 3). Neptune et al. (1997) also find RF to contribute to both Ext and Ant in forward pedaling.

Directionally sensitive expression of the biomechanical functions in the motor output pattern may appear not only in muscles showing large changes in phasing (e.g., SM and RF) but also in muscles showing invariance in phasing. For example, TA and MG may also contribute to another biomechanical function (Flex) in addition to Dorsi and Plant functions, respectively (Fig. 3B). The expression of Flex, primarily in the backward direction, is consistent with the EMG signal energy in backward pedaling being unaccounted for by a phase shift. The ability of TA to contribute to Flex is consistent with the increase in crank torque and TA activity seen in one-legged pedaling (Ting et al. 1998). These task-dependent expressions of biomechanical functions in the motor output may arise from modulation of the neural elements responsible for the expression of the functions in the output.

Comparison to walking

Activity of muscles during forward and backward walking can also be categorized into similar biomechanical functions, with some having to change in phasing during a reversal in walking direction. Extensor muscles (e.g., vasti and gluteus maximus) are active in stance in forward and backward walking to produce, putatively, limb extension (Ext function). Thus the Ext function does not change phasing in walking, although burst durations in extensor muscles may be directionally sensitive (Thorstensson 1986; Winter et al. 1989). Iliopsoas and iliacus are active during swing in forward walking to produce limb flexion (Flex function) and alternate with extensors (Perry 1992; Rose and Gamble 1994). In walking, acceleration of the limb in the anterior and posterior directions occur at opposite limb extension/flexion transitions compared with pedaling because of differences in the biomechanics. For example, in forward walking the foot is accelerated anteriorly with respect

to the pelvis at the extension-to-flexion transition, which is opposite to forward pedaling. Thus the Ant and Post functions in walking with respect to limb extension and flexion are opposite compared with pedaling, although as in pedaling they reverse with direction. Consistent with RF and HAM contributing to Ant and Post functions, respectively, they tend to be active at the appropriate transitions in forward walking (e.g., Nilsson et al. 1985; Perry 1992; Rose and Gamble 1994) and tend to shift phase in backward walking (Deursen et al. 1998; Duysens et al. 1996; Thorstensson 1986; Winter et al. 1989). During walking, RF typically has another burst during stance, which corresponds with Ext (Nilsson et al. 1985; Shiavi 1990; Thorstensson 1986; Winter et al. 1989). Similar to pedaling, the RF burst during stance (Ext function) is emphasized in backward walking (Deursen et al. 1998; Thorstensson 1986; Winter et al. 1989), although at higher forward walking speeds and in forward running, the RF burst during anterior transitions may increase in prominence (Nilsson et al. 1985). In addition, reflex modulation in RF and HAMS appears to reverse in backward walking (Duysens et al. 1996). In contrast to pedaling, however, phase shifts are typically seen in ankle muscles when walking direction is reversed (Deursen et al. 1998; Thorstensson 1986; Winter et al. 1989), which may be consistent with the reversal in ankle power (Winter et al. 1989).

Backward walking may, therefore, require a reversal in phasing of two biomechanical function pairs (Plant/Dorsi as well as Ant/Post) instead of just one (Ant/Post) as in pedaling, with the phasing of the Ext/Flex pair immutable to walking direction. A control scheme for walking composed of two main components (i.e., some biomechanical functions that change in phasing with walking direction and others that do not) is compatible with the finding that forward and backward walking can be characterized by just two features of the motor output (Deursen et al. 1998). Similarly, in salamanders, one principal feature, correlated with muscles undergoing a phase shift, can describe the EMG differences in forward and backward walking (Ashley-Ross and Lauder 1997).

Neural strategy for locomotion

The biomechanical function pairs (Ext-Flex, Ant-Post, and Dorsi-Plant) form a basis for a control strategy of forward and backward pedaling, which may also apply to walking. Reflex modulation in pedaling (e.g., Brown and Kukulka 1993; for review see Brooke et al. 1997) is very similar to that in walking (e.g., Yang and Stein 1990) and suggests a common neuronal basis. On the basis of the hindlimb locomotion of decorticate cats, a similar division of the locomotor cycle into flexion, extension, and two overlapping transition regions was proposed, with biarticular and more distal muscles acting primarily during the transitions (cf. Fig. 1A with Fig. 10 from Perret and Cabelguen 1980). The three pairs of alternating functions are similar in concept to Grillner's (1981) unit-burst generators or other concepts of mutually inhibitory neuronal elements (e.g., Stein and Smith 1997). However, the elements in our scheme are organized by biomechanical function rather than by muscle anatomy. Loeb (1984) also proposed compartmentalization of neuromuscular control based on function.

The phasing of the biomechanical function pairs could be achieved through three pairs of mutually inhibitory neuronal elements. However, the neural circuitry producing the 25%

phase shift between either Ant-Post or Plant-Dorsi and Ext-Flex (Fig. 1A) may be more complex than the mutually inhibitory connections proposed by Grillner (1981) to exist among the unit burst generators (cf. schema for 25% phase shift in swimmerets) (Skinner et al. 1997). Similar to the concepts of Grillner (1981), connections between the biomechanical function pairs must be reconfigured, depending on the locomotor task and direction. In forward pedaling, Ant and Dorsi are excited concurrently (and out-of-phase with Post and Plant), suggesting possible mutually excitatory and inhibitory interconnections between these functions. In backward pedaling, these interconnections must be opposite. The setting of the configuration of the interconnections among the biomechanical function elements is likely under supraspinal control with afferent modulation (e.g., Grillner 1981; Grillner and Dubuc 1988; Rossignol et al. 1988).

The scheme proposed, although largely maintaining opposition of traditional antagonistic elements, allows for the flexibility in muscle excitation often observed. Task-dependent modulation of the expression of a function in the motor output provides a muscle with the capability to participate in one function at times and another function at other times. In contrast, the strict extensor-flexor groupings proposed by Grillner (1981) cannot account for the sometimes "paradoxical" activity of biarticular muscles classified as either extensor or flexor according to anatomy (e.g., HAMS in pedaling) (Gregor et al. 1985). Specifically, both biarticular muscles, e.g., RF in human walking (Nilsson et al. 1985), ST in cat walking (Loeb 1984), and RF in rat locomotion (Leon et al. 1994), and monoarticular muscles, e.g., SL in pedaling (Neptune et al. 1997) and VL in rat locomotion (Leon et al. 1994), may have multiple bursts. In our scheme, multiple bursts (or bursts of differing durations) are to be expected as both biarticular and uniarticular muscles can contribute to the execution of multiple functions. Others proposed that biarticular muscle activity is highly mutable (Smith 1987) and may receive inputs from both flexor and extensor half-centers (Perret and Cabelguen 1980), compatible in concept with our scheme of muscles being able to contribute to multiple functions. Because multiarticular muscles develop torques at more than one joint, they will tend to have multiple functions, although loading conditions (e.g., interactions with the environment) can affect the functions of both mono- and biarticular muscles (e.g., Zajac and Gordon 1989). Modulation of the neural elements controlling the expression of the functions in the motor output provides the control scheme with the ability to execute a variety of tasks.

Conclusion

A locomotor strategy based on control of biomechanical functions derived from computer simulations of pedaling was found to be compatible with forward and backward pedaling. Each of the six functions is proposed to alternate with only one other function to form three biomechanical function pairs. This strategy predicts well the phasing of muscles during these tasks. In pedaling, a reversal in phasing of one biomechanical function pair is suggested. Because some muscles can participate in the execution of more than one biomechanical function, complex changes in the phasing of a muscle can and do occur with a change in pedaling direction. Similarities between

pedaling and walking suggest that a similar strategy may be operational in both tasks.

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REFERENCES

- ANDREWS, J. G. The functional roles of the hamstrings and quadriceps during cycling: Lombard's Paradox revisited. *J. Biomech.* 20: 565–575, 1987.
- ASHLEY-ROSS, M. A. AND LAUDER, G. V. Motor patterns and kinematics during backward walking in the Pacific giant salamander: evidence for novel motor output. *J. Neurophysiol.* 78: 3047–3060, 1997.
- BROOKE, J. D., CHENG, J., COLLINS, D. F., MCLROY, M. E., MISIASZEK, J. E., AND STAINES, W. R. Sensori-sensory afferent conditioning with leg movement: gain control in spinal reflex and ascending paths. *Prog. Neurobiol.* 51: 393–421, 1997.
- BROWN, D. A. AND KUKULKA, C. G. Human flexor reflex modulation during cycling. *J. Neurophysiol.* 69: 1212–1224, 1993.
- BUFORD, J. A. AND SMITH, J. L. Adaptive control for backward quadrupedal walking. II. Hindlimb muscle synergies. *J. Neurophysiol.* 64: 756–766, 1990.
- CARLSOO, S. AND MOLBECH, S. The functions of certain two-joint muscles in a closed muscular chain. *Acta Morphol. Neerlando-Scand.* 6: 377–386, 1966.
- VAN DEURSEN, R.W.M., FLYNN, T. W., MCCRORY, J. L., AND MORAG, E. Does a single control mechanism exist for both forward and backward walking? *Gait Posture* 7: 214–224, 1998.
- DUYSENS, J., TAX, A. A., MURRER, L., AND DIETZ, V. Backward and forward walking use different patterns of phase-dependent modulation of cutaneous reflexes in humans. *J. Neurophysiol.* 76: 301–310, 1996.
- FREGLY, B. J. *The Significance of Crank Load Dynamics to Steady-State Pedaling Biomechanics: An Experimental and Computer Modeling Study* (PhD thesis). Stanford, CA: Stanford University, 1993.
- FREGLY, B. J. AND ZAJAC, F. E. A state-space analysis of mechanical energy generation, absorption, and transfer during pedaling. *J. Biomech.* 29: 81–90, 1996.
- GREGOR, R. J., CAVANAGH, P. R., AND LAFORTUNE, M. Knee flexor moments during propulsion in cycling—A creative solution to Lombard's Paradox. *J. Biomech.* 18: 307–316, 1985.
- GRILLNER, S. Control of locomotion in bipeds, tetrapods, and fish. In: *Handbook of Physiology: The Nervous System. Motor Control*. Washington, DC: Am. Physiol. Soc., 1981, sect. 1, vol. II, chapt. 26, p. 1179–1236.
- GRILLNER, S. AND DUBUC, R. Control of locomotion in vertebrates: spinal and supraspinal mechanisms. In: *Advances in Neurology*, edited by S. G. Waxman. New York: Raven, 1988, vol. 47, p. 425–453.
- VAN INGEN SCHENAU, G. J. On the action of biarticular muscles, a review. *Neth. J. Zool.* 40: 521–540, 1990.
- JORGE, M. AND HULL, M. L. Analysis of EMG measurements during bicycle pedaling. *J. Biomech.* 19: 683–694, 1986.
- KAUTZ, S. A. AND BROWN, D. A. Relationships between timing of muscle excitation and impaired motor performance during cyclical lower extremity movement in post-stroke hemiplegia. *Brain* 121: 515–526, 1998.
- LOEB, G. E. The control and responses of mammalian muscle spindles during normally executed motor tasks. *Exerc. Sport Sci. Rev.* 12: 157–204, 1984.
- LEON, R. DE, HODGSON, J. A., ROY, R. R., AND EDGERTON, V. R. Extensor- and flexor-like modulation within motor pools of the rat hindlimb during treadmill locomotion and swimming. *Brain Res.* 654: 241–250, 1994.
- NEPTUNE, R. R., KAUTZ, S. A., AND HULL, M. L. The effect of pedaling rate on coordination in cycling. *J. Biomech.* 30: 1051–1058, 1997.
- NEWMILLER, J., HULL, M. L., AND ZAJAC, F. E. A mechanically decoupled two force component bicycle pedal dynamometer. *J. Biomech.* 21: 375–386, 1988.
- NILSSON, J., THORSTENSSON, A., AND HALBERTSMA, J. Changes in leg movements and muscle activity with speed of locomotion and mode of progression in humans. *Acta Physiol. Scand.* 123: 457–475, 1985.
- PERRET, C. AND CABELGUEN, J. M. Main characteristics of the hindlimb locomotor cycle in the decorticate cat with special reference to bifunctional muscles. *Brain Res.* 187: 333–352, 1980.
- PERRY, J. *Gait Analysis: Normal and Pathological Function*. New York: McGraw-Hill, 1992.
- POZZO, T., BERTHOZ, A., AND LEFORT, L. Head stabilization during various locomotor tasks in humans. I. Normal subjects. *Exp. Brain Res.* 82: 97–106, 1990.
- PRATT, C. A., BUFORD, J. A., AND SMITH, J. L. Adaptive control for backward quadrupedal walking V. Mutable activation of bifunctional thigh muscles. *J. Neurophysiol.* 75: 832–842, 1996.
- RAASCH, C. C. *Coordination of Pedaling: Functional Muscle Groups and Locomotor Strategies* (PhD thesis). Stanford, CA: Stanford University, 1996.
- RAASCH, C. C., ZAJAC, F. E., MA, B., AND LEVINE, W. S. Muscle coordination of maximum-speed pedaling. *J. Biomech.* 30: 595–602, 1997.
- ROSSIGNOL, S., LUND, J. P., AND DREW, T. The role of sensory inputs in regulating patterns of rhythmic movements in higher vertebrates. In: *Neural Control of Rhythmic Movements in Vertebrates*, edited by A. H. Cohen, S. Rossignol, and S. Grillner. New York: Wiley, 1988, p. 201–283.
- ROSE, J. AND GAMBLE, J. G. *Human Walking*. Baltimore: Williams & Wilkins, 1994.
- RYAN, M. M. AND GREGOR, R. J. EMG profiles of lower extremity muscles during cycling at constant workload and cadence. *J. Electromyog. Kinesiol.* 2: 69–80, 1992.
- SHIAMI, R. Electromyographic patterns in normal adult locomotion. In: *Gait in Rehabilitation*, edited by G. L. Smidt. New York: Churchill Livingstone, 1990, p. 99–119.
- SKINNER, F. K., KOPELL, N., AND MULLONEY, B. How does the crayfish swimmeret system work? In sights from nearest-neighbor coupled oscillator models. *J. Comput. Neurosci.* 4: 151–160, 1997.
- SMITH, J. L. Hindlimb locomotion of the spinal cat: synergistic patterns, limb dynamics and novel blends. In: *Neurobiology of Vertebrate Locomotion*, edited by S. Grillner, P.S.G. Stein, H. Forssberg, D. G. Stuart, and R. M. Herman. London: MacMillan, 1987, p. 185–200.
- STEIN, P.S.G. AND SMITH, J. L. Neural and biomechanical control strategies for different forms of vertebrate hindlimb motor tasks. In: *Neurons, Networks, and Motor Behavior*, edited by P. S. Stein, S. Grillner, A. I. Selverston, and D. G. Stuart. London: MIT Press, 1997, p. 61–73.
- THORSTENSSON, A. How is the normal locomotor program modified to produce backward walking? *Exp. Brain Res.* 61: 664–668, 1986.
- TING, L. H. *Neural Strategies for Control of Locomotion Elucidated by Novel Pedaling Paradigms* (PhD thesis). Stanford, CA: Stanford University, 1998.
- TING, L. H., RAASCH, C. C., BROWN, D. A., KAUTZ, S. A., AND ZAJAC, F. E. Sensorimotor state of the contralateral leg affects ipsilateral muscle coordination of pedaling. *J. Neurophysiol.* 80: 1341–1351, 1998.
- VILENSKY, J. A., GANKIEWICZ, E., AND GEHLSSEN, G. A kinematic comparison of backward and forward walking in humans. *J. Hum. Mov. Stud.* 13: 29–50, 1987.
- WINTER, D. A., PLUCK, N., AND YANG, J. F. Backward walking: a simple reversal of forward walking? *J. Mot. Behav.* 21: 291–305, 1989.
- YAMAGUCHI, G. T. AND ZAJAC, F. E. Restoring unassisted natural gait to paraplegics via functional neuromuscular stimulation: a computer simulation study. *IEEE Trans. Biomed. Eng.* 37: 886–902, 1990.
- YANG, J. F. AND STEIN, R. B. Phase-dependent reflex reversal in human leg muscles during walking. *J. Neurophysiol.* 63: 1109–1117, 1990.
- ZAJAC, F. E. AND GORDON, M. Determining muscle's force and action in multi-articular movement. *Exerc. Sport Sci. Rev.* 17: 187–230, 1989.
- ZERNICKE, R. F. AND SMITH, J. L. Biomechanical insights into neural control of movement. In: *Handbook of Physiology*, edited by L. B. Rowell and J. T. Shepherd. New York: Oxford Univ. Press, 1996, sect. 12, p. 293–330.