Mutability of Bifunctional Thigh Muscle Activity in Pedaling due to Contralateral Leg Force Generation

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INTRODUCTION

In cat locomotion, Smith and colleagues have demonstrated that the extremely variable activity of bifunctional thigh muscles seems to be related to adapting to the task-specific intersegmental mechanical demands (for review, Stein and Smith 1997; Zernicke and Smith 1996). In humans, it has been suggested that bifunctional muscles are primarily responsible for the control of the direction of external forces (e.g., Ingen Schenau et al. 1992) and the fine-tuning of muscle coordination (Zajac 1993). Others have focused on the potential energy efficiency of bifunctional muscles when movements are performed with the combination of a hip flexor and knee extensor joint moment (or vice versa) (Prilutsky et al. 1998; Wells 1988). Our laboratory has suggested that the bifunctional thigh muscles are the dominant contributors to uninterrupted limb transitions (Raasch and Zajac 1999; Rausch et al. 1997; Ting et al. 1999).

Pratt et al. (1996) have proposed that this mutability reflects a more complex range of flexor- and extensor-related inputs of increased relative strength arising from peripheral, and perhaps central, sources to the motoneurons innervating bifunctional muscles. While bifunctional motoneurons are thought to receive excitatory inputs from both the flexor and extensor locomotor half centers (Perret and Cabelguen 1980), the central influences are likely less important because bifunctional muscle activity appears to be so closely linked with the intersegmental mental dynamics and external forces (Pratt et al. 1996). Thus motion- and force-related afferent information plays a critical role in shaping this complex activity (Ingen Schenau et al. 1992) and the fine-tuning of muscle coordination (Zajac 1993). Others have focused on the potential energy efficiency of bifunctional muscles when movements are performed with the combination of a hip flexor and knee extensor joint moment (or vice versa) (Prilutsky et al. 1998; Wells 1988). Our laboratory has suggested that the bifunctional thigh muscles are the dominant contributors to uninterrupted limb transitions (Raasch and Zajac 1999; Rausch et al. 1997; Ting et al. 1999).

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One potential shaping influence on the activity of bifunctional muscles that has not received much investigation is the afferent and efferent inputs associated with the contralateral limb that are specifically related to transitions between limb

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Flexion and extension. Human locomotion requires that uninterrupted transitions between extension and flexion (and vice versa) occur in each leg and be tightly coordinated with the performance of the opposite leg (e.g., walking with one leg is impossible). Independent rhythm generation in each hindlimb of spinal cats has been demonstrated both in split-belt treadmill conditions where the legs can walk at different speeds (Forsberg et al. 1980) and in experiments where one hindlimb is prevented from moving while the other continues rhythmic behavior (Duysens and Pearson 1980; Grillner and Rossignol 1978). However, it has been proposed that the central pattern generators for the hindlimbs of spinal turtles may be part of a shared bilateral core in which some of the neurons involved in the pattern generation of one leg also participate in producing the normal motor rhythm for the contralateral leg (Stein and Smith 1997; Stein et al. 1995). Regardless of the existence of direct bilateral coupling of central pattern generation, it is clear that contralateral afferent information has an important role in shaping the ipsilateral motor pattern. For example, unilateral deafferentation in spinal cats disrupts both ipsi- and contralateral stepping (Giuliani and Smith 1987). Thus influences from the contralateral sensorimotor state likely affect the motor pattern of the ipsilateral leg during human locomotion. However, whether bifunctional motoneurons in human subjects are particularly influenced by peripheral inputs from the contralateral leg has not been addressed.

Interlimb effects on the human locomotor pattern have been investigated with split belt treadmills (e.g., Dietz 1994; Jensen 1998) and split-crank pedaling ergometers (Ting et al. 1998, 2000). The split-belt treadmill experiments demonstrated flexibility in the timing of stance-swing transitions and differential interlimb influences on antagonistic leg muscle activation, but the mechanical coupling that exists between the loading of the two legs complicates interpretation (Dietz et al. 1994). Split-crank pedaling, in contrast, allows decoupling of the mechanical loading (for a detailed review, see Ting et al. 2000). Furthermore, activity in the bifunctional muscles during pedaling is well understood in relation to the task mechanics, as rectus femoris provides anteriorly directed leg acceleration during the flexion-to-extension transition and the hamstrings group provide posteriorly directed leg acceleration during the extension-to-flexion transition (Neptune et al. 1997, 2000; Rasch and Zajac 1999; Ting et al. 1999). Studying only the effects during limb flexion, Ting et al. (2000) showed in split-crank pedaling experiments that contralateral sensorimotor state strongly influenced bifunctional muscle activity in the pedaling leg. But bifunctional muscles principally propel the crank during the limb transitions, not during limb flexion, and how their activity is affected during the limb extension/flexion transitions is unknown.

The purpose of this study was to determine whether contralateral rhythmic force generation substantially shapes bifunctional thigh muscle activity during the limb transition regions in pedaling (i.e., regions where the bifunctional thigh muscles exert their primary effects on propulsion). We hypothesized that during a unilateral pedaling task rhythmic activity in the nonpedaling leg would support the ongoing timing and amplitude of bifunctional thigh muscle activity in the pedaling leg during the transition phases of the pedaling cycle. We further hypothesized that the alterations in muscle activity would contribute to improved task performance, as measured by net mechanical work done by the pedaling leg.

**Methods**

Fifteen healthy subjects (11 male, 4 female; ages 30.8 ± 6.7 (SD) years; height = 1.76 ± 0.08 (SD) m; mass = 73.9 ± 9.5 (SD) kg) gave informed consent to participate in the study. The study was approved by the Institutional Review Board of the Stanford University Medical School.

**Experimental setup and data collection**

We developed a two-servomotor, split-axle pedaling apparatus to reproduce the mechanical load of bilateral pedaling throughout the whole crank cycle, not just the flexion phase (cf. Ting et al. 2000). Because each crank is connected to its own servomotor, we were able to implement different control modes using the custom hardware and software. The cranks arms of the split-axle pedaling apparatus were uncoupled and each driven by a toothed-belt drive (4:1 ratio) from independent 9 kW servomotors (Kollmorgen B606A motor, D20 motor controller, 1-kHz servo loop; Kollmorgen Motion Technologies Group, Commack, NY). The data acquisition and servomotor control was implemented with LabVIEW 5.0 software. Custom real-time C software, accessible from LabVIEW, provided dual-motor servocontrol and data-acquisition for 32 analog channels and 4 encoder channels at a 1-kHz sample rate.

Servomotor control was implemented to produce loads on the right pedaling leg that replicated the dynamics encountered with a conventional coupled-crank ergometer (i.e., flywheel inertia, belt friction, and freewheeling). The emulated frictional load, at 60 rpm, dissipated ~80 J, and the emulated conventional-ergometer inertia resulted in an intra-cycle variation in crank angular velocity of typically ±6 rpm (not too dissimilar from pedaling a conventional ergometer).

In the coupled-crank pedaling trials, the servomotors emulated conventional two-legged coupled-crank ergometry pedaling. Thus the servomotors were programmed to fix the relationship between the two cranks, as in the one-axle crank of standard ergometry pedaling (i.e., 180° anti-phased), and to use the force each leg exerted on its crank to accelerate the “one-axle emulated” crank. The right servomotor was programmed so that the forces applied to both pedals accelerated the right crank. With the left crank maintained 180° anti-phased and the right crank responsive to forces on both pedals, there was no remaining degree of freedom, so the left crank was also responsive to the forces on both pedals.

In the pseudo-pedaling and unilateral pedaling trials, the servomotors were programmed so that the right pedal force accelerated the right crank; the left pedal force had no effect on the acceleration of either crank; and the load encountered by the right pedaling leg was identical to the load a leg encounters during conventional two-legged ergometry pedaling. The load encountered during conventional two-legged ergometry pedaling is not only the ergometer load (see preceding text), but also the load transmitted through the one-axle crank from the contralateral pedaling leg (e.g., the contralateral leg provides an assistance crank torque to lift the leg against gravity during ipsilateral limb flexion). Thus the right servomotor was programmed to also emulate the crank torque generated by the contralateral leg. A generic one-legged crank torque profile (i.e., torque as a function of crank angle) was generated from previously recorded two-legged pedaling data and used for all subjects.

In the pseudo-pedaling trials, the left crank was position-servocontrolled to be 180° offset from the right crank and the subjects were instructed to pedal with both legs just as in the coupled-crank pedaling trials. However, in contrast to coupled-crank pedaling, acceleration of the “one-axle emulated” crank only resulted from the right pedal force and not the left pedal force. The right servomotor emulated the production of crank torque by a generic left leg instead. Thus force

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generation in the pseudo-pedaling left leg had no mechanical effect on crank rotation. Pilot work suggested that, as long as pedaling is initiated with the right leg, subjects do not perceive pseudo-pedaling as different from coupled-crank pedaling.

In the unilateral pedaling trials, the left crank was position-servoed to remain fixed and stationary. The servomotors were programmed so that the isotonic isometric force generated by the left leg had no mechanical effect on the right pedaling crank.

Subjects wore cleated ankle braces (DePuy Orthotech, Tracy CA) on each leg. The left brace was free and analogous to a cleated cycling shoe during the coupled-crank and pseudo-pedaling trials and fixed when it was stationary during the unilateral pedaling trials. Thus the configuration of the leg (hip and knee angles) was uniquely determined by the crank angle (e.g., Redfield and Hull 1986). Subjects were seated during all trials and restrained by a hip belt to reduce pelvis motion. Subjects sat with a forward lean of ~10°, which is a typical trunk angle during walking (Pozzo et al. 1990), and supported some of their torso weight on the handlebars (Ting et al. 1999).

Normal and shear peak forces were measured using pedal dynamometers (Newmiller et al. 1988). Crank and pedal angles were measured using digital optical encoders. Surface EMGs were measured from four muscles bilaterally: vastus medialis (VAS), rectus femoris (RF), biceps femoris long head (BF), and semimembranosus (SM). All signals were sampled at 1,000 Hz. Analog RC anti-aliasing filters with a cutoff frequency of 80 and 800 Hz were used on non-EMG and EMG channels, respectively, to reduce high-frequency noise from the servomotor power amplifiers (~20 kHz). The particulars of our measurements are similar to those of our recent studies (Ting et al. 1999, 2000).

Experimental trials

Five trials were collected in the following order: one trial—coupled-crank pedaling (15-s duration); one trial—pseudo-pedaling (15-s duration); and three randomly assigned trials—unilateral pedaling with contralateral rhythmic isometric force generation (35-s duration). The workload of 80 J roughly corresponds to a moderate touring pace (Macintosh et al. 2000). The moderate workload, combined with instructions to ask for additional rest if fatigued, suggest that subjects were unlikely to be affected by fatigue.

The coupled-crank pedaling and pseudo-pedaling trials were used to investigate whether pseudo-pedaling produces the same motor output in the right leg as coupled-crank pedaling.

The three unilateral pedaling trials with contralateral rhythmic isometric force generation were used to investigate the influence of contralateral sensorimotor activity on bilateral muscle activity (Fig. 1). The left crank was held stationary by its servomotor at one of three different crank angles (0°, 90°, and 180°, see Fig. 2) with the left foot attached to the crank by an ankle brace. To mimic the natural joint angles during pedaling, the ankle was set to neutral in the plantarflexion/dorsiflexion position except for the 180° crank position, which was set to 20° plantarflexion. We refer to the extension-to-flexion transition as the “anterior” transition because the leg is moving posteriorly during its execution. Similarly, the flexion-to-extension transition is referred to as the “anterior” transition. The subjects were instructed to time contralateral isometric force production to coincide with the time of execution of the antagonistic function by the pedaling leg. Thus isometric forces that would act to propel the crank during the anterior transition, limb extension and the posterior transition were to be executed by the contralateral stationary left leg while the pedaling right leg executed the posterior transition, limb flexion, and anterior transition, respectively (Fig. 1). The stationary contralateral leg was relaxed for the 15 s of the trial and then it was generating isometric force for the last 20 s.

The five experimental trials resulted in six conditions used in data analysis. The six conditions were: coupled-crank pedaling, pseudo-pedaling, unilateral pedaling with the stationary contralateral leg relaxed, and unilateral pedaling with the stationary contralateral leg in three different configurations generating rhythmic isometric force. Data from each condition of each subject were averaged over 10 consecutive crank revolutions. Note that the mean values for the “unilateral pedaling with the contralateral leg relaxed” condition were calculated from the first 15 s of each of the isometric force generation trials using a total of 30 revolutions, (i.e., 10 revolutions in each of the 3 isometric force generation trials). The mean values for the “unilateral pedaling with contralateral force generation” trials were calculated from the last 10 consecutive revolutions in the trial. Each trial used a metronome for ~10 s to establish a steady cadence at 60 rpm with data collection commencing afterward.

Data processing

Crank torque was calculated from pedal force and crank and pedal angle measurements after they were downsampl ed to 200 Hz and low-pass filtered using a zero-lag Butterworth filter (20-Hz cutoff for forces and 8-Hz cutoff for angles). Crank torque is the product of the crank arm length (which is constant) and the component of pedal force that accelerates the crank (i.e., the tangential crank force). Crank torque is an important indicator of mechanical output (and similarly tangential crank force) because the area under the crank torque trajectory over a crank cycle is the net external work output by that leg during that revolution. EMG signals were high-pass filtered with a Butterworth filter (20-Hz cutoff, 0 lag) to remove low-frequency servomotor noise and movement artifacts. Mean EMG signal offset
Average tangential crank force in each quadrant (as defined by right crank angle) was calculated instead of work output because no mechanical work is done when the crank is stationary. Left leg average EMGs coincident with each pedaling leg quadrant were also calculated to confirm excitation of the muscles that contribute to production of crank torque during that quadrant during pedaling.

**Data analysis**

Normalized work output and normalized average EMGs were analyzed in each quadrant to answer our primary research question: does contralateral force generation alter bifunctional thigh muscle activity in the limb transition regions? We performed a two-factor ANOVA analysis (blocked by subject) to test for differences in the average EMG of each muscle in the pedaling leg during its primary quadrant of activity (i.e., Q1 for RF; Q2 for VM; and Q3 for BF and SM) for average EMG of each muscle and differences in the mechanical work output during the two transition quadrants (Q1 and Q3). Dunnett’s post hoc test ($P < 0.05$) was used to test for differences between the mean of the reference condition (unilateral pedaling with the contralateral leg at rest) and that of each other condition (3 conditions of unilateral pedaling with contralateral isometric force generation).

Normalized work output and normalized average EMGs were analyzed to answer two additional questions to verify our experimental design: did subjects use the same motor pattern in the right leg during pseudo-pedaling as during coupled-crank pedaling? We again performed a two-factor ANOVA analysis (blocked by subject) to identify mean differences in the mechanical work output and the average EMGs of the right leg in each quadrant. The second question was did the subjects execute the contralateral force generation as directed? We performed a two-factor ANOVA analysis (blocked by subject) for each of the three contralateral isometric force generating conditions to identify mean differences in the left leg crank force in the targeted quadrant compared with each of the other quadrants. Dunnett’s post hoc test ($P < 0.05$) was used to test for differences between the mean of the target quadrant and that of each other quadrant.

**RESULTS**

The motor pattern of the right pedaling leg was virtually identical in pseudo-pedaling and coupled-crank pedaling. No differences in mechanical work production (Fig. 3) or in EMGs existed in any of the four quadrants between coupled-crank pedaling and pseudo-pedaling ($P > 0.05$). The EMG patterns (Fig. 4) were also similar to those previously re-
ported during bilateral (coupled-crank) pedaling on a conventional ergometer (e.g., Neptune et al. 1997; Ting et al. 1999). Notice that group averages of BF and SM activity do not show a strongly phasic pattern and exhibit high variability. However, inspection of data from individual subjects reveals that nearly all subjects do indeed exhibit phasic activity, which apparently is masked in the group averages because of the high variability found among subjects in onset and offset of BF and SM activity (note that comparisons are done between trials for individual subjects and the group data are only shown for illustration). Because these muscles are known to be quite variable (Ryan and Gregor 1992), the EMGs found in our study reflect a behavior consistent with that of previous studies. Because the motor pattern in pseudo-pedaling and coupled-crank pedaling was identical, we concluded that the split-axle servomotor system emulated well both the load of a conventional ergometer and the crank torque load typically produced by a contralateral pedaling leg.

The subjects were successful in generating the desired rhythmic isometric force with the contralateral leg while the right leg pedaled. Subjects produced significantly greater tangential crank force in the targeted quadrant \( P < 0.05 \) than in the other three quadrants (Fig. 5), with the only exception being that Q4 was not greater than Q1 for the extension isometric condition. Furthermore, the dominant muscles generating the tangential crank force, as assessed by EMG (Fig. 5), are those known to produce the tangential crank force when a pedaling leg is in the same configuration (Neptune et al. 2000; Raasch et al. 1997). Thus the isometric force was produced predominantly by the same muscles and would have accelerated the crank during the region had it not been fixed in place. There-
fore we use “contralateral anterior transition (or extension or posterior transition) force generation” to refer to the contralateral leg generating rhythmic isometric force with the same muscles the leg does in pedaling when it is in a configuration corresponding to where the anterior transition (or extension or posterior transition) is performed.

Bifunctional muscle activity and crank work output increased significantly in the pedaling leg when the stationary contralateral leg generated rhythmic anterior or posterior transition force [e.g., Fig. 6, RF increases in Q1 (see boxed region) compared with RF when contralateral leg (CL) is relaxed; BF and SM increase in Q3]. Contralateral anterior transition force generation increased by 42% the percentage of the total work done by the pedaling leg that was done in Q3 (from 26 to 37%, \( P \leq 0.0001 \)), and the increased work was associated with activity increases of 145% in the bifunctional RF and 124% in semimembranosus (135–331%, \( P < 0.0001 \); 122–273%, \( P < 0.0006 \); note percentage is relative to Q3 average EMG during bilateral pedaling; Fig. 7). Contralateral posterior transition force generation increased by 175% the percentage of the total work done in the pedaling leg that was done in Q1 (from 4 to 11%, \( P < 0.0001 \)), and the increased work was associated with 76% increased activity in the bifunctional RF (116–204%, \( P < 0.0006 \); note percentage is relative to Q1 average EMG during bilateral pedaling) (Fig. 7).

There were no significant changes in bifunctional muscle activity and crank work output in the pedaling leg when the stationary contralateral leg generated rhythmic extension force. However, there were observed minor increases in all bifunctional muscle activity and associated crank work output. Contralateral extension force generation increased RF activity in Q1 and increased BF and SM activity in Q3. The increased bifunctional muscle activity in Q1 and Q3 were associated with an increase in work output in those quadrants corresponding to the limb transitions.

**DISCUSSION**

Mutability of bifunctional muscle activity as a result of contralateral force generation

Bifunctional thigh muscle activity, which is principally responsible for uninterrupted anterior (limb flexion-to-extension) and posterior (limb extension-to-flexion) transitions, was highly mutable as different conditions of contralateral isometric force generation resulted in dramatically different levels of EMG activity. The anterior transition is predominantly performed by RF and the posterior transition by hamstrings (Nepf et al. 2000; Raasch et al. 1997; Ting et al. 1999). We found that contralateral isometric force generation enhanced significantly the execution of the limb transitions of the ipsilateral pedaling leg, as assessed by mechanical work done during the limb transitions and the activity of the bifunctional muscles. Specifically, we found that the rhythmic isometric generation of the contralateral anterior (or posterior) transition force significantly increased the execution of the posterior (or
anterior) transition of the ipsilateral pedaling leg. A similar but much less dramatic increased execution of the anterior and posterior transitions occurred in the pedaling leg with rhythmic isometric contralateral extension force generation. Further, when any of the three contralateral isometric forces were generated, the excitation of each of the ipsilateral bifunctional muscles always increased (although it did not always reach significance) in the primary phase where it contributes most to pedaling performance (e.g., crank output). These results suggest that, in humans, contralateral sensorimotor activity strongly facilitates the bifunctional muscle execution of the lower limb anterior and posterior transitions.

In contrast, the observed changes in activity of the unifunctional vastus medialis were much smaller in magnitude and much less common. Thus the results suggest that bifunctional muscles were controlled differently than the unifunctional muscles that execute limb extension.

Investigation of contralateral influences mediated via interlimb neural pathways was possible because the split-axle twoservomotor system eliminated the mechanical transmission of forces from one leg to another through the crank and allowed the pedaling leg to experience a load identical to conventional pedaling. The pseudo-pedaling condition allowed the contralateral leg to “participate” in bilateral pedaling (e.g., it was antiphased to the ipsilateral leg, and could generate force, as if pedaling) while the ipsilateral pedaling leg remained isolated from the mechanical performance of the contralateral leg (i.e., any force generated by the contralateral leg had no effect on rotation of either crank). We found no differences in the EMG or pedal force data for the right leg between pseudo-pedaling and crank-coupled (normal) pedaling. Thus the servomotor system reproduced the mechanical load on the pedaling leg during conventional bilateral pedaling. We were able to attribute the effects of the contralateral leg force generation to
interlimb neural pathways because of the ability of our servomotor apparatus to replicate the two-legged mechanical load during unilateral pedaling, a mechanical decoupling not possible during conventional two-legged pedaling or walking, even on a split-belt treadmill.

Possible influences unrelated to normal control of pedaling

We speculate that the strong enhancement of the ongoing timing and amplitude of bifunctional muscle activity due to the contralateral isometric force generation reflects an influence of sensorimotor activity that is similarly operational during normal pedaling. However, the influence may instead be through circuitry that is either distinct from that used in pedaling generation or gated differently than during pedaling. For example, it has been shown in the upper limbs that rhythmic contralateral isometric force generation strongly influences the muscle activation profile and movement pattern of a rhythmically moving ipsilateral limb. However, the influence on the stability characteristics of the coordination dynamics differed from the influence on the stability characteristics when both limbs were isometric or when both limbs were moving (Peper and Carson 1999). A suggested mechanism for this differential effect on stability is the presence of spinal mechanisms that modulate the gain of transmission to the motoneuron pool (via both afferent and descending pathways) differentially during isometric and shortening contractions. In particular, the gain of transmission of afferent input from the contralateral limb may differ when the ipsilateral limb is moving dynamically as opposed to generating isometric force.

Some of the changes in coordination occurring when only one leg pedals could be due to task-dependent differences in descending drive. For example, Oda (1997) found evidence that the bilateral strength deficit in human upper limbs (reduced maximal force output of one limb when comparing bilateral vs. unilateral performance) was associated with reduced premotor cortex activation. The implication was that the force deficit between the two conditions also resulted from changes in the motor command to an arm instead of from changes located

FIG. 7. Changes in crank mechanical work and EMG in the unilateral pedaling leg when the contralateral leg is no longer relaxed but instead generates contralateral force in one of three directions. Change is represented by the subtraction of each subject’s contralateral force generation condition from that subject’s contralateral relaxed condition. For each condition (column), a schematic at top shows the contralateral leg performing the commanded force generation, and the quadrant of the pedaling leg coinciding with the timing of contralateral leg force generation is shaded. Solid black bars represent significant differences ($P < 0.05$). Mechanical work in a quadrant is normalized by the total mechanical work done for a revolution and expressed as a percentage. Average EMG in a quadrant is normalized by the average EMG during the main quadrant of coupled-crank pedaling and expressed as a percentage. Note that while 100% implies that EMG increased by an amount equal to the amount occurring during normal coupled-crank pedaling, it does not imply a change of 100% because the EMG for unilateral pedaling with the contralateral leg relaxed differed from that in coupled-crank pedaling. During contralateral anterior transition force generation there were very dramatic facilitations of biceps femoris and semimembranosus that were associated with increased work output. During contralateral posterior transition force generation there was a facilitation of rectus femoris that was associated with increased work output. The effects in vastus medialis were much smaller, and the scale is magnified 4 times to show changes.
Implications for neural control of limb transitions

In humans, the bifunctional thigh muscles are extremely well suited to contribute to limb transitions between flexion and extension because of their ability to accelerate the foot (the end point of the leg) anteriorly (RF) or posteriorly (hamstrings) with respect to the pelvis. When movement is not allowed (e.g., quiet stance or isometric force generation), the bifunctional muscle action instead results in directing the ground contact force in the anterior and posterior directions. Also, the dominant periods of bifunctional muscle activity during normal walking occur during limb transitions, from late swing into the early loading phase of stance for hamstrings and from the preswing period of late stance phase into initial swing for RF (e.g., Perry 1992; Winter 1991).

The results of this study are consistent with the hamstrings and RF femoris muscles for each leg being organized into an anterior-posterior transition reciprocal pair that receives strong facilitation for the amplitude of ongoing activity due to the contralateral sensorimotor activity. Each muscle contributing to the execution of anterior and posterior transitions showed increased excitation due to contralateral posterior and anterior isometric force generation, respectively [Fig. 7; e.g., RF femoris excitation increased during the anterior transition (Q1) as a result of contralateral posterior transition force generation]. Because contralateral motor activity cannot be isolated from loading related sensory feedback, it is not possible to determine whether the sensorimotor activity influence is most strongly related to efferent or afferent activity.

Grillner (1981) hypothesized that the motor pattern for a leg might result from the combined activity of several unit burst generators, which he proposed would drive the flexors or extensors at one joint. Further, the unit burst generators could be organized as reciprocal pairs of anatomical antagonists at each joint. A unit burst-generator organization has also been used to describe pattern generators in several preparations (e.g., in turtles, Stein et al. 1995).

We propose that a framework based on the unique action of the bifunctional muscles have on accelerating the endpoint of the limb orthogonal to the extension-flexion pair will prove more functional than the single-joint oriented framework of a conventional unit burst generator organization. We propose the anterior-posterior bifunctional muscle pair organization because we feel that the bifunctional muscles contributing to this pair do not fit meaningfully into the single-joint oriented framework. Kumamoto et al. (1994) have presented mechanical engineering analyses (theoretical and a robot implementation) whose results suggest that the existence of an antagonistic pair of bifunctional muscles positively contributes to the compliant properties of a multiarticular limb and allows independent control of position and force at the limb end point.

In conclusion, contralateral sensorimotor activity strongly facilitates the activity of bifunctional thigh muscles perhaps because of their importance to the execution of the leg extension-flexion transitions. Further investigation into the control of bifunctional muscles during locomotion should consider the influences of contralateral sensorimotor activity because it is especially well suited for fine tuning the coordination of effective transitions between extension and flexion in a reciprocal gait. Human walking mechanics are inherently bilateral and strong interlimb coupling is needed to ensure that both legs are not in extension phase or flexion phase simultaneously. We believe that a better understanding of the influence of sensorimotor activity on the contralateral motor pattern has the potential to provide valuable new directions in the rehabilitation of persons with neurological deficits.

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CONTRALATERAL INFLUENCE ON BIFUNCTIONAL MUSCLE ACTIVITY


