

Contralateral Movement and Extensor Force Generation Alter Flexion Phase Muscle Coordination in Pedaling

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Ting, Lena H., Steven A. Kautz, David A. Brown, and Felix E. Zajac. Contralateral movement and extensor force generation alter flexion phase muscle coordination in pedaling. *J Neurophysiol* 83: 3351–3365, 2000. The importance of bilateral sensorimotor signals in coordination of locomotion has been demonstrated in animals but is difficult to ascertain in humans due to confounding effects of mechanical transmission of forces between the legs (i.e., mechanical interleg coupling). In a previous pedaling study, by eliminating mechanical interleg coupling, we showed that muscle coordination of a unipedal task can be shaped by interlimb sensorimotor pathways. Interlimb neural pathways were shown to alter pedaling coordination as subjects pedaling unilaterally exhibited *increased* flexion-phase muscle activity compared with bilateral pedaling even though the task mechanics performed by the pedaling leg(s) in the unilateral and bilateral pedaling tasks were identical. To further examine the relationship between contralateral sensorimotor state and ipsilateral flexion-phase muscle coordination during pedaling, subjects in this study pedaled with one leg while the contralateral leg either generated an extensor force or relaxed as a servomotor either held that leg stationary or moved it in antiphase with the pedaling leg. In the presence of contralateral extensor force generation, muscle activity in the pedaling leg during limb flexion was *reduced*. Integrated electromyographic activity of the pedaling-leg hamstring muscles (biceps femoris and semimembranosus) during flexion decreased by 25–30%, regardless of either the amplitude of force generated by the nonpedaling leg or whether the leg was stationary or moving. In contrast, rectus femoris and tibialis anterior activity during flexion decreased only when the contralateral leg generated high rhythmic force concomitant with leg movement. The results are consistent with a contralateral feedforward mechanism triggering flexion-phase hamstrings activity and a contralateral feedback mechanism modulating rectus femoris and tibialis anterior activity during flexion. Because only muscles that contribute to flexion as a secondary function were observed, it is impossible to know whether the modulatory effect also acts on primary, unifunctional, limb flexors or is specific to multifunctional muscles contributing to flexion. The influence of contralateral extensor-phase sensorimotor signals on ipsilateral flexion may reflect bilateral coupling of gain control mechanisms. More generally, these interlimb neural mechanisms may coordinate activity between muscles that perform antagonistic functions on opposite sides of the body. Because pedaling and walking share biomechanical and neuronal control features, these mechanisms may be operational in walking as well as pedaling.

INTRODUCTION

Recent findings about the ability to improve the locomotor capacity of individuals with spinal cord injury through the

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application of principles derived from pattern generator theory (for review, see Rossignol et al. 1996) underscore the necessity to better understand interlimb coordination mechanisms in humans; this would lead to the development of more effective rehabilitation strategies. The human spinal cord may possess some ability to produce bilateral locomotor activity (Calancie et al. 1994; Harkema et al. 1997; Rossignol et al. 1996) as shown in a number of vertebrates (for review, see Rossignol 1996). How such centrally generated signals are integrated with peripheral afferent information to produce coordinated bilateral locomotion remains elusive, especially in humans. However, motor patterns produced by individuals with spinal cord injury depend on bilateral sensory information associated with limb movement and loading (Harkema et al. 1997).

In vertebrate preparations, no clear picture of how sensory information modulates ipsi- and contralateral patterns exists. Evidence from spinal cats show that locomotor activity in each hindlimb can be generated independently (e.g., Grillner and Zangger 1979). Ipsilateral sensory feedback has been shown to be important in reinforcing locomotor activity, and both ipsilateral hip angle and loading of extensors affect ipsilateral phase changes from stance to swing in cat (Duysens and Pearson 1980; Grillner and Rossignol 1978; Pearson et al. 1992). In split-belt treadmill conditions, independent rhythm generation in each hindlimb is demonstrated by the ability of the hindlimbs to walk at different speeds (Forssberg et al. 1980). Further, one hindlimb can continue rhythmic behavior even when the other is prevented from doing so (Duysens and Pearson 1980; Grillner and Rossignol 1978). On the other hand, in similar cat preparations, interdependence of sensorimotor signals in the two hindlimbs is demonstrated by the maintenance of integral (e.g., 1:1 or 1:2) step frequencies, which ensures that one foot is always on the ground (Forssberg et al. 1980). Following unilateral deafferentation in spinal cats, disruption of both ipsi- and contralateral stepping occurs; this further illustrates the contralateral influence of afferent input (Giuliani and Smith 1987). In turtles, bilateral coupling of centrally generated rhythmic output is also demonstrated because spinal cord hemisection alters bilateral fictive rhythmic activity (Stein et al. 1995).

Elucidation of interlimb neural coupling mechanisms in humans is even more challenging because central and peripheral influences cannot be explicitly isolated. Changes in muscle coordination of a leg in unilateral tasks compared with similar bilateral tasks may be caused by two major factors: 1) contralateral sensorimotor signals mediated through neural inter-

limb coupling mechanisms and 2) ipsilateral afferent signals triggered by the forces transmitted to the ipsilateral leg due to the acceleration or movement of the contralateral leg. Although clear evidence for neural interlimb coupling has been demonstrated in static tasks in which no loadsharing occurs between the limbs (Howard and Enoka 1991; Schantz et al. 1989; Secher et al. 1988), results from dynamic tasks are not as conclusive. For example, though perturbations in stance elicit bilateral electromyographic (EMG) responses of similar latencies (Berger et al. 1984; Dietz and Berger 1982), the EMG changes in the nonperturbed leg may be due to afferent signals generated in that leg as a consequence of the instantaneous joint reaction forces generated in both legs, and the subsequent motion of the limb segments in the nonperturbed leg (Yamaguchi and Zajac 1990; Zajac 1993). Therefore mechanical and neuronal coupling can simultaneously affect muscle coordination of movement, making it difficult to isolate the effects of either factor. Nevertheless it seems reasonable that coordinative neuronal coupling would be effective in recovery from tripping or other perturbations to normal gait (e.g., Berger et al. 1984; Dietz et al. 1986; Eng et al. 1994).

Pedaling is a useful paradigm in the study of human locomotion. Task mechanics can be controlled and manipulated. The alternating flexion and extension of the limbs, characteristic of many modes of locomotion, can be studied without the confounding influence of balance. Phasing and frequency of leg movements are similar in walking and pedaling. Further, because the subject is seated, neither balance nor body-weight support is required, and the kinetics and kinematics of the legs can be analyzed in isolation of the head, arms, and trunk. In both pedaling and walking, significant forces are generated by the legs and applied to the environment during the extension phase, and passive or external forces tend to flex the limb during the flexion phase (Eng et al. 1997; Kautz and Hull 1993). In addition, many reflexes such as the H reflex and flexor reflex are modulated over the gait cycle and similarly modulated over the pedaling cycle (e.g., Brown and Kukulka 1993; for review, see Brooke et al. 1997). Thus neuronal elements responsible for gait may participate in pedaling tasks as well.

This study focused on neural interlimb coupling mechanisms that operate during the flexion phase in steady-state pedaling because a previous pedaling study (Ting et al. 1998b) found that the most significant difference between bilateral and unilateral pedaling occurs in the flexion phase. Ting et al. proposed that sensorimotor signals associated with contralateral extension play a role in modulating flexion-phase muscle activity in pedaling. Because force and movement may provide powerful influences on the ongoing locomotor pattern, the effects of contralateral movement and extensor force production on muscle activity in the flexion phase during unilateral pedaling were investigated. The sensorimotor conditions in the contralateral nonpedaling leg were designed to mimic pedaling in the amount and timing of the generation of extensor force, the largest component of muscular force production during pedaling (Kautz and Hull 1993; Raasch et al. 1997), and/or in the antiphasing of the movement of the legs. Specifically, we hypothesized that isolated generation of forces and/or passive movements of the contralateral nonpedaling leg would inhibit the flexion phase activity normally present in a unilateral

pedaling task. Abstracts of this work have appeared (Ting et al. 1997, 1998a).

METHODS

Eighteen healthy subjects [10 male, 8 female; age, 22 ± 3 (SD) years; height, 1.7 ± 0.7 (SD) m; weight, 65 ± 8 (SD) kg] who rode a bicycle for <50 miles/wk and who were naive to the experimental goals signed consent forms prior to participation in the study. This study was approved by the Institutional Review Board (Medical Committee for the Protection of Human Subjects in Research) at Stanford University Medical School.

The pedaling leg (left leg) of each subject performed the same pedaling task in all trials, while the condition of the nonpedaling (right leg) leg was varied. The conditions of the nonpedaling leg were chosen such that the effects of leg movement and extensor force generation in that leg on flexion-phase coordination of the pedaling leg could be tested. The interaction effects of nonpedaling leg force and movement were also tested along with the effect of force level (i.e., low vs. high relative to typical forces encountered during pedaling) and rhythmicity (i.e., rhythmic application of force).

Experimental apparatus

A bicycle ergometer was modified so subjects would pedal against the same mechanical load profile for all eight conditions. The left and right cranks were mechanically uncoupled. Thus the right leg could not mechanically influence left leg pedaling coordination. In addition, the kinematic relationship between the left and right cranks could be manipulated using a servomotor. Subjects were linked to the cranks via clipless pedals and standard bicycling cleats; thus the feet maintained contact with the pedals at all times.

The left crank propelled a flywheel, which was removed from a Monark bicycle ergometer. A constant-force spring (or a negator spring, i.e., a spring that develops the same force irrespective of its length), attached to the left crank arm (Fig. 1A), provided an approximately sinusoidal crank torque that impeded propulsion during extension ($0-180^\circ$, Fig. 3A) and aided propulsion during flexion ($180-360^\circ$). This sinusoidal load pattern approximately replicated the alternating pattern of retarding and propulsive torque generated by the right leg in two-legged pedaling (Fig. 1A). The peak crank torque contributed by the spring (22 N-m) was chosen such that the leg would be propelled to overcome gravity in the flexion phase. Thus as in two-legged pedaling, subjects could have executed the pedaling task with little active flexion.

The nonpedaling (right) crank was controlled by a programmable servomotor (Kollmorgen B606A motor, D20 motor controller, 2 kHz servo loop; Kollmorgen Motion Technologies Group, Commack, NY), which either fixed the nonpedaling crank in a static position or moved the crank at a 180° phase relation to the opposite (left) crank (Fig. 1B). In the movement condition, the motor was servocontrolled by the optical encoder signal from the opposite (left) pedaling-leg crank. As a result, torque applied by the nonpedaling leg did not contribute to crank propulsion because all torque generated by the nonpedaling leg was resisted by the motor as it maintained the 180° phase relation with the pedaling crank. The motor was also used in a control condition where it rotated the crank at a constant 60 rpm.

Subjects wore a cleated cycling shoe on the pedaling foot and a cleated ankle brace (DePuy Orthotech, Tracy, CA) fixed at 10° plantarflexion on the nonpedaling leg (Fig. 1B). By fixing the ankle angle, the configuration of the leg (hip and knee angles) is uniquely determined by the crank angle (Fregly and Zajac 1996; Kautz and Hull 1993; Redfield and Hull 1986). Thus no muscular effort was required to maintain a static configuration when the crank position was fixed on the nonpedaling side. Further, no muscular effort was required to maintain a comfortable limb trajectory when the crank was moved by the motor. Because the relationship between contralateral extension

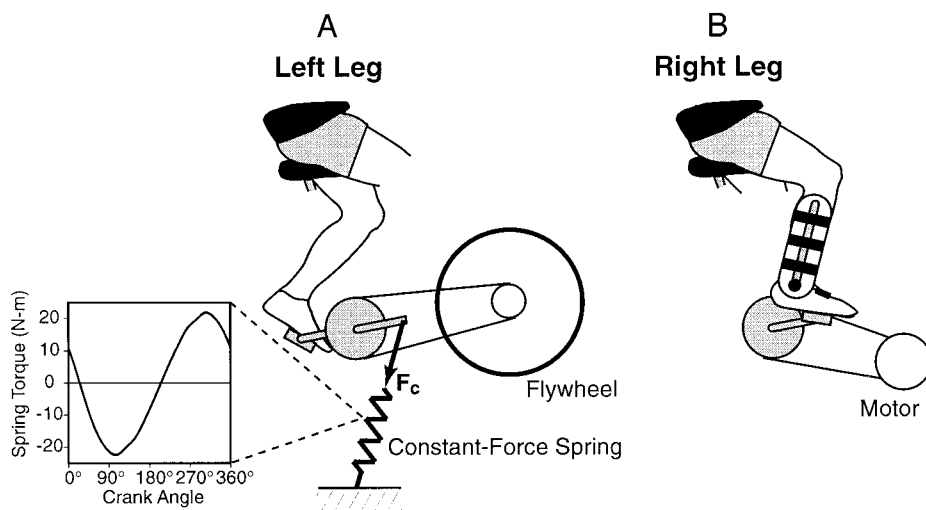


FIG. 1. Bicycle ergometer with independent cranks. A: the left leg pedals against a flywheel load as in a typical exercise bicycle. A constant-force spring provides propulsion to the leg during limb flexion so that, as in 2-legged pedaling, subjects are not required to contribute to crank propulsion during flexion. The spring also provides resistance during limb extension as does the weight of the contralateral limb in 2-legged pedaling. *Inset*: 20 consecutive cycles of crank torque generated by the spring. B: the right crank is controlled by a servomotor, which either holds the crank stationary or moves the crank 180° out-of-phase with the left crank. Mechanical coupling or load sharing through the cranks is, therefore prevented. The right ankle is braced. Thus no muscle activity is required to stabilize the right leg, regardless of whether the leg is stationary or moving.

and ipsilateral flexion was being explored, the ankle angle of the brace was set to 10° plantarflexion to correspond to the position the ankle has in the mid-extension phase during pedaling (~107°, Fig. 3A) (Nordeen-Snyder 1977). Subjects were seated during all trials and wore a hip belt to reduce pelvic 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. 1998b).

Pedal forces were measured using pedal dynamometers on both the pedaling and nonpedaling crank (Newmiller et al. 1988). A load cell measured the force of the constant force spring. Crank and pedal angles from both sides were measured using digital optical encoders (4096 counts/revolution). A linear transducer was attached to the hip belt over the anterior superior iliac spine (ASIS) of the nonpedaling leg, which measured the amplitude of ASIS movement in its primary direction of movement which is forward, downward and laterally (cf. Neptune and Hull 1995). This measure of ASIS movement was used to compare pelvis motion between different trial conditions.

Surface EMGs were measured from seven muscles bilaterally: vastus medialis (VM), left (LVM) and right (RVM); rectus femoris (RF), left (LRF) and right (RRF); biceps femoris long head (BF), left (LBF) and right (RBF); semimembranosus (SM), left (LSM) and right (RSM); tibialis anterior (TA), left (LTA) and right (RTA); medial gastrocnemius (MG), left (LMG) and right (RMG); and soleus (SL), left (LSL) and right (RSL).

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 very high-frequency noise from the motor (~20 kHz).

Practice protocol

Subjects were trained to pedal with their pedaling leg so that they could maintain a constant cadence of 60 rpm without using any feedback. A preliminary trial oriented subjects to the apparatus and ensured that seat and handlebar heights were appropriate. Subjects pedaled bilaterally with the motor driving the right crank antiphase to the left pedaling-crank encoder signal. Subjects perceive this situation as normal two-legged pedaling. A metronome helped subjects maintain a steady cadence during the first 40 s of the trial. Next, five practice trials of 60-s duration of unilateral pedaling were presented to subjects. The metronome usage duration was decreased incrementally from 40 to 10 s across the five trials. To avoid cumulative fatigue, subjects rested for ≥ 1 min between each practice trial.

After the practice session, subjects were able to pedal smoothly and consistently at a steady cadence between 55 and 65 rpm. Smoothness was determined by the absence of freewheeling, which is a decoupling

of the crank from the flywheel load that occurs when the crank decelerates relative to the flywheel (for discussion, see Fregly and Zajac 1996; Raasch 1995). In a few cases, subjects did not perform consistently after five practice trials and were given additional practice trials.

Next, to familiarize subjects with the sensation of having their right leg moved by a motorized crank, the nonpedaling crank was rotated by the motor at 60 rpm so subjects would be able to relax their right leg in subsequent movement conditions when requested. During this practice trial the pedaling leg was relaxed with the pedaling crank fixed in a horizontal, mid-extension position (~107° crank angle).

Finally, subjects practiced using the vertical force-feedback indicator employed during the experimental conditions. Both pedaling and nonpedaling cranks were locked at mid-extension (~107° crank angle). The level of downward force being exerted perpendicular to the surface of the pedal of the nonpedaling leg was displayed on a computer monitor, which displayed a vertical bar. The vertical bar was divided into five regions. Each bar was illuminated when the force reached the weight of the leg resting on the pedal at mid-extension plus a specified amount. Two of the bars were larger in height to indicate a larger range of force. These were the "target" zones of the high- and low-force levels. The three smaller bars served to indicate when the subject exceeded or fell short of the targets. The high-force level corresponded to the force on the pedal during mid-extension of pedaling [~300 N; i.e., (leg weight + 150 N) to (leg weight + 450 N)]. The low level was just slightly above the weight of the leg [i.e., (leg weight + 25 N) to (leg weight + 100 N)]. The height of the force windows were chosen such that changes in force due to subtle movement or shifting of position of the right leg would not cause the subject to exit the desired force range. Further, it was important that subjects could generate the force easily and naturally, as in normal pedaling, exerting as little cognitive control over force level as possible. Four 20-s practice trials were performed. Subjects were asked to maintain a tonic level of extensor force in the high and then low target range for the duration of the trial. Then they were asked to generate rhythmic extensor force (paced by a 1-Hz metronome), first to the high target and then to the low target.

Experimental conditions

Eight trial conditions and one additional control condition were presented to subjects in random order. In all but the control condition, the pedaling leg pedaled at 60 rpm. Each trial condition was given a two-letter code indicating the state of the nonpedaling leg (Fig. 2): either static (S) or moving (M) and either generating a force (F) or relaxed (R). A subscript was used to indicate tonic (T) or rhythmic (R) force with a capital letter to designate a high level of force and a

		Static		Moving				
		SR	MR	SF _r	MF _r			
Force Generation	Relaxed	SR	MR			A		
		Rhythmic	high				SF _R	MF _R
	low		SF _r			MF _r		
	Tonic	high	SF _T					C
		low	SF _t					

FIG. 2. Sensorimotor state of the contralateral (right) nonpedaling leg. The sensorimotor state of the nonpedaling leg in each condition is represented by 1 cell of the grid. In all these conditions the ipsilateral (right) pedaling leg pedaled at 60 rpm. *A*: 4 primary conditions tested the effects of contralateral movement and rhythmic force generation on pedaling coordination. In the nominal condition, SR, the nonpedaling leg is relaxed and held in the mid-extension pedaling position. In SF_R, a high rhythmic extensor force is generated by the stationary nonpedaling leg concomitant with the flexion phase of the pedaling leg, consistent with the phasing of force generation in 2-legged pedaling. In MR and MF_R, the nonpedaling leg is moved 180° out-of-phase with the pedaling leg, as in 2-legged pedaling. In MR, the leg is relaxed while moved. In MF_R, subjects generated a high rhythmic extensor force while the leg is moved. *B*: conditions SF_r and MF_r tested whether contralateral low-force generation was sufficient to affect pedaling performance. *C*: the effect of tonic force generation by the contralateral, stationary, nonpedaling leg on pedaling coordination was tested. In SF_T, subjects generated a high level of force; in SF_t, a low level of force. All conditions were presented in random order. State of nonpedaling leg: static (S) or moving (M) generating either a force (F) or relaxed (R). Subscripts denote tonic (T) or rhythmic (R) force with high or low levels of force represented with an upper- or lowercase letter.

lower-case letter to designate a low level of force. In the cases where the nonpedaling leg was static, the nonpedaling crank was maintained in the horizontal position (107°), which corresponds approximately to mid-extension in pedaling. In the movement conditions, the nonpedaling crank was servomoved antiphase to the left crank. In the cases where the nonpedaling leg was relaxed and did not generate force, the subject was instructed to neither resist nor aid the motion imposed by the motor. In force-generating conditions, subjects used the force feedback indicator to achieve the desired force level.

Four trial conditions were used to investigate the importance of contralateral nonpedaling extensor force generation and movement on flexion-phase coordination of the ipsilateral pedaling leg (Fig. 2A). The nonpedaling leg was either static and relaxed (SR; i.e., the nominal condition), moving and relaxed (MR), static and producing a high rhythmic isometric extensor force (SF_R), or moving and producing a high rhythmic extensor force (MF_R). During rhythmic force production, subjects were instructed to push downward with the nonpedaling leg concurrent to the flexion phase of the pedaling leg, such that the timing would be similar to that of two-legged pedaling. Thus subjects were asked to generate an extensor force to the high-force target.

Two additional trial conditions were used to determine the effect of extensor force level produced by the nonpedaling leg. Subjects generated a rhythmic force with the contralateral nonpedaling leg static or moving, as before, but only to the low-force target (SF_r, MF_r).

Finally, two other trial conditions were used so that the effect of the rhythmic nature of force generation compared with tonic force generation could be studied. In these two conditions, subjects maintained a constant force level with the nonpedaling leg throughout the pedaling cycle (SF_T, SF_t, Fig. 2C). This was only done in the static condition because additional constraint and movement-dependent forces on the pedal (Kautz and Hull 1993) make it impractical to

measure constant force production by the subjects when the leg is moving. Further, subjects would have had to execute the difficult task of resisting the motor while simultaneously allowing the motor to move the nonpedaling leg.

In the “control” condition (MRØ), the usually pedaling leg was stationary and relaxed while the nonpedaling leg, also relaxed, was moved at 60 rpm by the motor for ~40 s. Notice that this “control” condition, where neither leg pedals, is different from the nominal trial condition (SR).

Each trial condition was also ~40 s in duration, with the metronome used in the first 10 s, and data collected in the last 20 s of the trial after the subjects had reached a steady-state cadence without the metronome. To minimize the effects of fatigue, subjects rested for at least one minute between trials.

Data processing

Force and angle data were downsampled to 200 Hz, low-passed filtered using a Butterworth filter (10-Hz cutoff, zero-lag), and used to calculate crank torque. Crank torque is the component of pedal force, multiplied by crank arm length, which accelerates the crank. All data were referenced to pedaling-leg crank angle, with 0° corresponding to the crank being closest to the seat (Fig. 3A). Crank angles between 0 and 180° refer to periods of leg extension, when the foot is moving

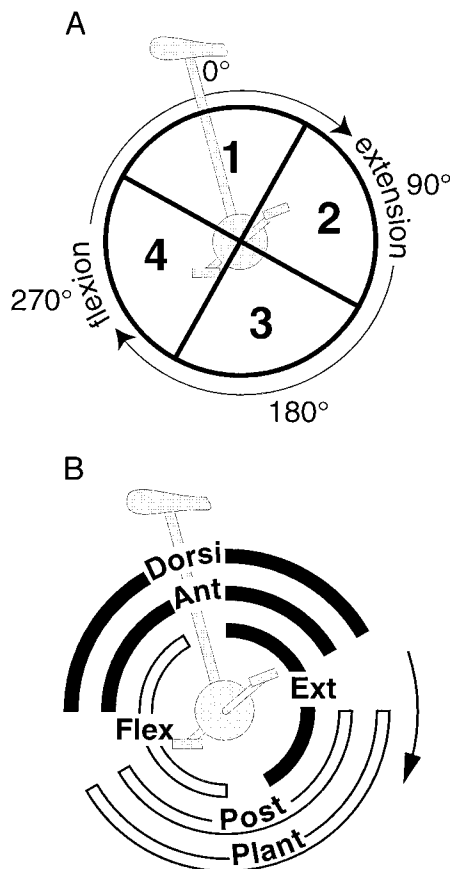


FIG. 3. Quadrants used to analyze muscle activity in the pedaling leg (*A*) and the corresponding functional muscle groups (*B*). Six functional muscle groups are sufficient to achieve a wide range of pedaling tasks (Raasch and Zajac 1999; Ting et al. 1999). Muscle activity was analyzed in quadrants centered on mid-phase of the functional muscle groups. Quadrant 4 corresponds to the phasing of the functional muscle group (Flex), which is responsible for accelerating the limb into flexion. The flexion phase is the phase of the cycle under investigation in this study. Ext muscles accelerate the leg into extension. Ant and Post muscles accelerate the leg anteriorly and posteriorly. Dorsi and Plant muscles accelerate the ankle into dorsi- and plantar flexion.

away from the pelvis. Crank angles between 180 and 360° refer to leg flexion, when the foot moves toward the pelvis. Data from each condition of each subject were averaged over 10 consecutive crank revolutions.

EMG signals were high-pass filtered with a Butterworth filter (35-Hz cutoff, 0 lag) to remove low-frequency motor noise. Mean signal offset was subtracted from the EMG signals and EMGs were rectified before further processing.

For data analysis, the signals measured during the pedaling crank cycle were divided into four quadrants (Fig. 3A) with each centered at mid-phase of one or two of the six biomechanical functions executed in forward pedaling (Fig. 3B) (Raasch and Zajac 1999; Raasch et al. 1997; Ting et al. 1999). Thus flexion-phase coordination of pedaling was quantified by analyzing data in quadrant 4, and changes in the extension-to-flexion phase were quantified by analyzing data in quadrant 3, etc. Data analysis focused on flexion-phase (quadrant 4) coordination.

Pedaling-leg integrated EMG (iEMG) and work output in each quadrant were calculated and averaged over all steady-state cycles (~20) to produce mean values for each subject and trial condition. The net work output by the pedaling leg in each quadrant is proportional to the average crank torque in the quadrant. Work output (workload) and iEMG over the entire cycle were found by summing the respective quantities over the four quadrants.

Performance of the nonpedaling leg was also monitored in each trial to ensure that the desired sensorimotor state was achieved. Mean extensor force generated by the nonpedaling leg concurrent with the flexion phase of the pedaling leg (quadrant 4) was calculated, along with iEMG from the nonpedaling leg and the standard deviation of ASIS motion on the nonpedaling side. Because EMG signals during static and dynamic conditions cannot be directly compared due to differences in motor unit and muscle recruitment (Gielen 1999; Theeuwens et al. 1994; van Bolhuis and Gielen 1997), comparison of nonpedaling EMGs among only static conditions, or among only movement conditions, were made.

Data analysis

Data were analyzed (2-way ANOVA with subject and trial condition as a factor) to answer the following questions:

1) Does nonpedaling leg movement and/or force generation affect flexion-phase coordination in the pedaling leg? [2-way ANOVA comparing only trial conditions SR, MR, SF_R, and MF_R to test independent and combined effects of movement and high rhythmic force generation (MR, SF_R, and MF_R) relative to the nominal condition (SR)].

2) Does the level of force generated by the nonpedaling leg affect flexion-phase coordination in the pedaling leg? (2-way ANOVA with trial conditions SF_R, MF_R, SF_T, and MF_T to test effects of high vs. low rhythmic force, with and without movement; and with trial conditions SR, MR, SF_T, and MF_T to test the effects of low rhythmic force vs. no force generation.)

3) Is the presence of force generation alone during nonpedaling leg extension sufficient to affect pedaling flexion-phase coordination or is the additional rhythmic nature of the force also contributory? Specifically, does tonic force generation have the same effect as rhythmic force generation? (2-way ANOVA with SF_R, SF_T, SF_T, and SF_T to test the effects of tonic vs. rhythmic force generation at high and low levels.)

RESULTS

Force data from the pedaling leg were only available for 14 of the 18 subjects due to a damaged wire. All other data, including pedaling-leg EMGs, were collected from all 18 subjects.

Performance of subject and experimental apparatus

The workload and cadence of the pedaling leg remained unchanged over all conditions in all subjects. The average workload for the subjects ranged from 79.7 to 82.1 J/cycle and was not significantly different for any condition ($P > 0.05$ for all pairwise comparisons). The work done by the constant force spring was also consistent across all conditions ($P > 0.05$ for all pairwise comparisons) and varied by <1% during any particular trial. Subjects were able to maintain a pedal cadence of ~60 rpm in all trials, with mean cadences per subject ranging from 59 to 67 rpm. ASIS motion was cyclical, generally moving forward and downward during the downstroke (cf. Neptune and Hull 1995) with peak forward displacement occurring when the crank was near bottom-dead-center (example: Fig. 4, A and B). Although hip movement was greater in movement conditions than in static conditions, there was no difference in amplitude of hip motion of the nonpedaling leg across all static trials or across all movement trials (Fig. 4C).

The servomotor was successful in achieving the desired isometric and movement conditions of the nonpedaling crank. During static conditions, the nonpedaling crank position was maintained in a horizontal position [$0.3 \pm 0.4^\circ$ (SD) average position error across all subjects]. The crank did not move appreciably as the standard deviation of movement within each trial was near zero ($0.07 \pm 0.05^\circ$ across all trials). In movement conditions, the desired 180° antiphase relationship was essentially maintained, as the average phase between left and right cranks across all trials was $176 \pm 5^\circ$, with an average standard deviation of $1.4 \pm 1.1^\circ$ within each trial.

Effects of nonpedaling leg movement and force generation on pedaling coordination

The condition where the nonpedaling leg was static and relaxed (SR) served as the nominal condition against which the movement and force generating conditions of the nonpedaling leg were compared. The flexion-phase torque profile and EMGs of the pedaling leg were similar to those reported previously for unilateral pedaling where the contralateral nonpedaling leg was in a similar sensorimotor state (Ting et al. 1998b). Crank torque in the flexion phase (quadrant 4) was near zero (example: Fig. 5A), and correspondingly, flexion-phase work output across all subjects was also about zero (Fig. 6A), which differs from the negative work output normally observed in two-legged pedaling (about -10 J) (Ting et al. 1998b).

Compared with the nominal condition (SR), passive movement (MR) of the nonpedaling leg was unsuccessful in reducing the crank torque and work output produced by the pedaling leg during its flexion phase [crank torque example from 1 subject: compare Fig. 5B (quadrant 4) with Fig. 5A (quadrant 4); work output across all subjects: Fig. 6A, compare MR with SR, $P > 0.05$]. Correspondingly, EMG activity in the pedaling leg during the flexion phase was also unchanged [example from 1 subject: compare Fig. 7B (quadrant 4) with Fig. 7A (quadrant 4); average iEMG across all subjects: Fig. 8, A-D, compare MR with SR, all $P > 0.05$].

In contrast, high rhythmic extensor force generation in the stationary nonpedaling leg (SF_R) was successful in reducing flexion-phase crank torque and work output in the pedaling leg

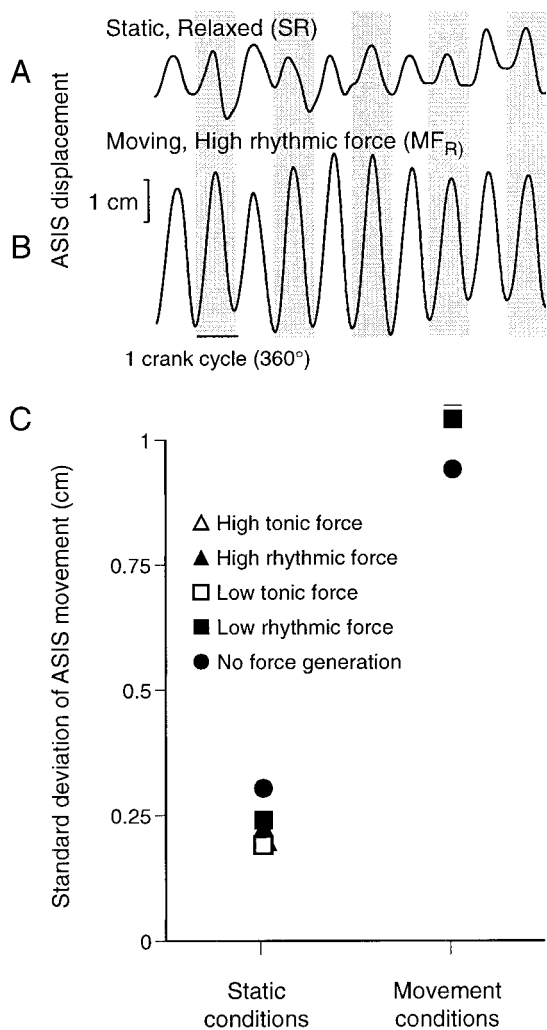


FIG. 4. Anterior superior iliac spine (ASIS) movement of the nonpedaling leg as an indication of pelvis motion. Representative trajectories of the ASIS in 1 subject when the nonpedaling leg was static and relaxed (SR; A) or moving and generating a high rhythmic force during the flexion phase of the pedaling leg (MF_R; B). Linear displacement of the ASIS was measured in the direction of maximum movement for each subject, approximately in the forward and downward direction (positive displacement in plot). One oscillation was observed per pedaling cycle with the maximum excursion occurring at mid-cycle when the pedaling-leg crank was at bottom-dead-center. Because the ASIS moved in a repeatable sinusoidal fashion, differences in the amount of motion of the ASIS were characterized by the standard deviation of the displacement trajectory (C). Motion of the ASIS was lower during static than during movement conditions. There was no significant difference in the standard deviation of ASIS movement for the static conditions, or for the movement conditions. Because pedaling-leg crank torque and muscle activity changed in only some of the movement conditions and in only some of the static conditions, the differences among conditions cannot be due to pelvis motion alone (see DISCUSSION).

compared with the nominal condition SR [crank torque example from 1 subject: compare Fig. 5C (quadrant 4) with Fig. 5A (quadrant 4); work output across all subjects: Fig. 6B, compare SF_R with SR, $P < 0.01$]. Correspondingly, EMG activity over the flexion phase decreased in some of the pedaling leg muscles, specifically in BF and SM [example from 1 subject, compare LBF and LSM in Fig. 7C (quadrant 4) with LBF and LSM in Fig. 7A (quadrant 4); average iEMG across all subjects: Fig. 8, A and B, compare SF_R with SR, both $P < 0.01$]. However, no reduction of iEMG activity in RF or TA over the

flexion phase were observed [example from 1 subject, compare LRF and LTA in Fig. 7C (quadrant 4) with LRF and LTA in Fig. 7A (quadrant 4); average iEMG across all subjects: Fig. 8, C and D, compare SF_R with SR, both $P > 0.05$].

The addition of movement to high rhythmic force generation in the nonpedaling leg (MF_R) was sufficient, however, to reduce RF and TA activity in the pedaling leg during its flexion phase [example from 1 subject, compare LRF and LTA in Fig. 7D (quadrant 4) with LRF and LTA in Fig. 7A (quadrant 4); average iEMG across all subjects: Fig. 8, C and D, compare MF_R with SR, $P < 0.05$ for LRF and $P < 0.01$ for LTA]. This was the only condition where RF and TA activity were reduced (Fig. 8, C and D: compare MF_R with the other conditions). This condition (MF_R) also reduced BF and SM activity in the pedaling leg [example from 1 subject, compare LBF and LSM in Fig. 7D (quadrant 4) with LBF and LSM in Fig. 7A (quadrant 4); average iEMG across all subjects: Fig. 8, A and B, compare MF_R with SR, both $P < 0.01$]. However, the addition of movement to the nonpedaling leg did not reduce further the reduction in BF and SM activity observed with high rhythmic force generation alone (Fig. 8, A and B, compare MF_R with SF_R, both $P > 0.05$). Similarly, flexion-phase work output during this condition of movement and high rhythmic force generation in the nonpedaling leg (MF_R) decreased compared with the nominal condition [crank torque example from 1 subject: compare Fig. 5D (quadrant 4) with Fig. 5A (quadrant 4); work output across all subjects: Fig. 6B, compare MF_R with SR, $P < 0.01$] but no more than the decrease observed with high rhythmic force generation (Fig. 6B, compare MF_R with SF_R, $P > 0.05$).

A low level of rhythmic force generation by the nonpedaling leg, whether the leg was moved (MF_r condition) or not (SF_r condition), was also effective in reducing both the flexion-phase work output in the pedaling leg (compare MF_r and SF_r in Fig. 6C with SR in Fig. 6A; both $P < 0.01$) and the activity in BF and SM (Fig. 8, A and B, compare MF_r and SF_r with SR; both $P < 0.01$) but was ineffective in reducing RF and TA activity (Fig. 8, C and D, compare MF_r and SF_r with SR; both $P > 0.05$). This reduction in BF and SM activity when rhythmic force generation was low did not differ from the decrease found when rhythmic force generation was high (Fig. 8, A and B, compare MF_r and SF_r with MF_R and SF_R; all $P > 0.05$). However, the reduction in flexion-phase work output in the static rhythmic low-force condition (SF_r) was less than the reduction in either the rhythmic high-force static condition (compare SF_r in Fig. 6C with SF_R in Fig. 6B; $P < 0.05$) or the rhythmic high-force moving-leg condition (compare SF_r in Fig. 6C with MF_R in Fig. 6B; $P < 0.05$). On the other hand, when movement was added to rhythmic low-force generation (MF_r condition), flexion-phase work output was reduced by an amount no less than that in the rhythmic high-force, static or moving, conditions (compare MF_r in Fig. 6C with SF_R or MF_R in Fig. 6B, both $P > 0.05$).

Compared with the nominal condition when the nonpedaling leg was stationary and relaxed (SR condition), no significant change in coordination of the pedaling leg during its flexion phase was detected when the nonpedaling leg generated a high or low tonic extensor force (SF_T and SF_t conditions). Neither was flexion-phase work output significantly changed (compare SF_T and SF_t in Fig. 6D with SR in Fig. 6A; both $P > 0.05$) nor

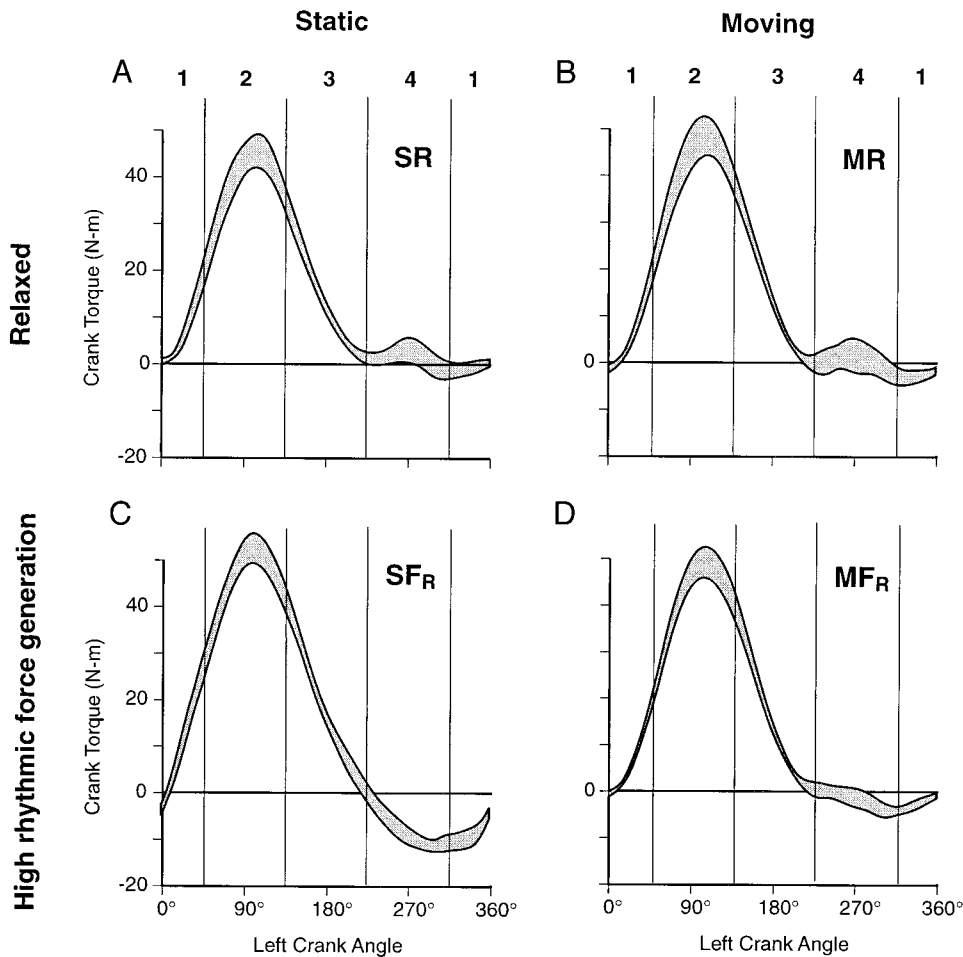


FIG. 5. Pedaling-leg (left) crank torque from 1 subject in the primary 4 conditions. Mechanical load on the left crank was the same during all conditions, but the sensorimotor state of the contralateral (right) nonpedaling leg varied. Gray areas represent means \pm 1 SD of crank torque, averaged over \sim 18 consecutive cycles per condition. A: SR (nominal condition where the nonpedaling leg is stationary and relaxed): crank torque during mid-flexion phase (quadrant 4) is \sim 0. B: MR (nonpedaling leg is servomoved and relaxed): crank torque during flexion (quadrant 4) does not differ from SR. C: SF_R (nonpedaling stationary leg generates high rhythmic extensor force): crank torque during flexion (quadrant 4) decreases; thus work output is negative. This crank torque is similar to that generated by 1 leg during 2-legged pedaling (Ting et al. 1998b). D: MF_R (nonpedaling servomoved leg generates high rhythmic extensor force): crank torque during flexion (quadrant 4) decreases. However, most subjects in contrast to this one generated negative crank torque comparable with that in SF_R.

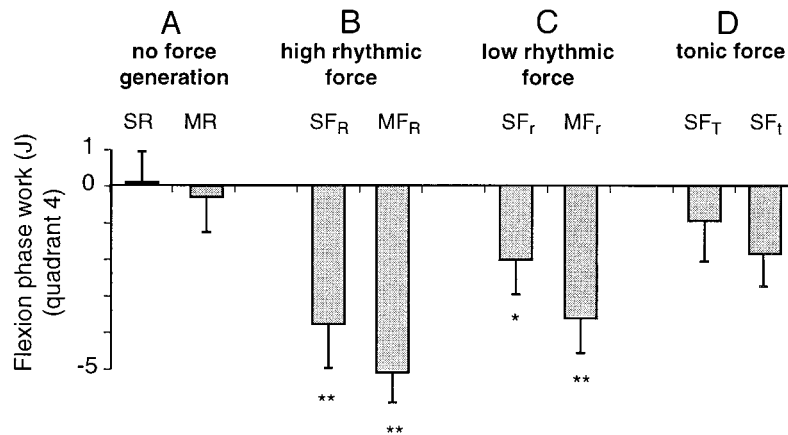


FIG. 6. Work output by the pedaling leg in the flexion phase (quadrant 4), averaged over all 14 subjects. Bars represent means \pm SE. ** Significant reduction ($P < 0.01$) in work output compared with the nominal condition (SR). * Significant reduction in work output compared with the SR condition but at a lower significance level ($P < 0.05$). A: no force generation in the nonpedaling leg: whether the nonpedaling leg is stationary (SR) or moving (MR), work is \sim 0 and not significantly different from each other ($P > 0.05$). B: high rhythmic force generation in the nonpedaling leg: whether the nonpedaling leg is stationary (SF_R) or moving (MF_R), work output is negative (thus the leg is propelled primarily by the constant force spring) and significantly lower than the nominal condition SR ($P < 0.01$). Work output in the 2 conditions (SF_R, MF_R) are not different from one other ($P > 0.05$). C: low rhythmic force generation in the nonpedaling leg: When the nonpedaling leg is stationary (SF_r), work output is also negative and significantly lower than the nominal condition SR ($P < 0.01$) but less than the high negative work output in the high-force-generating condition SF_R ($P < 0.05$). When the nonpedaling leg is moving (MF_r), work output is again negative and significantly lower than the nominal condition SR ($P < 0.01$), but no different from the high negative output in the high-force-generating condition MF_R ($P > 0.05$). D: tonic force generation in the stationary nonpedaling leg: no difference in work output compared with the nominal condition (SR) exists with either high (SF_T) or low (SF_t) tonic force generation ($P > 0.05$).

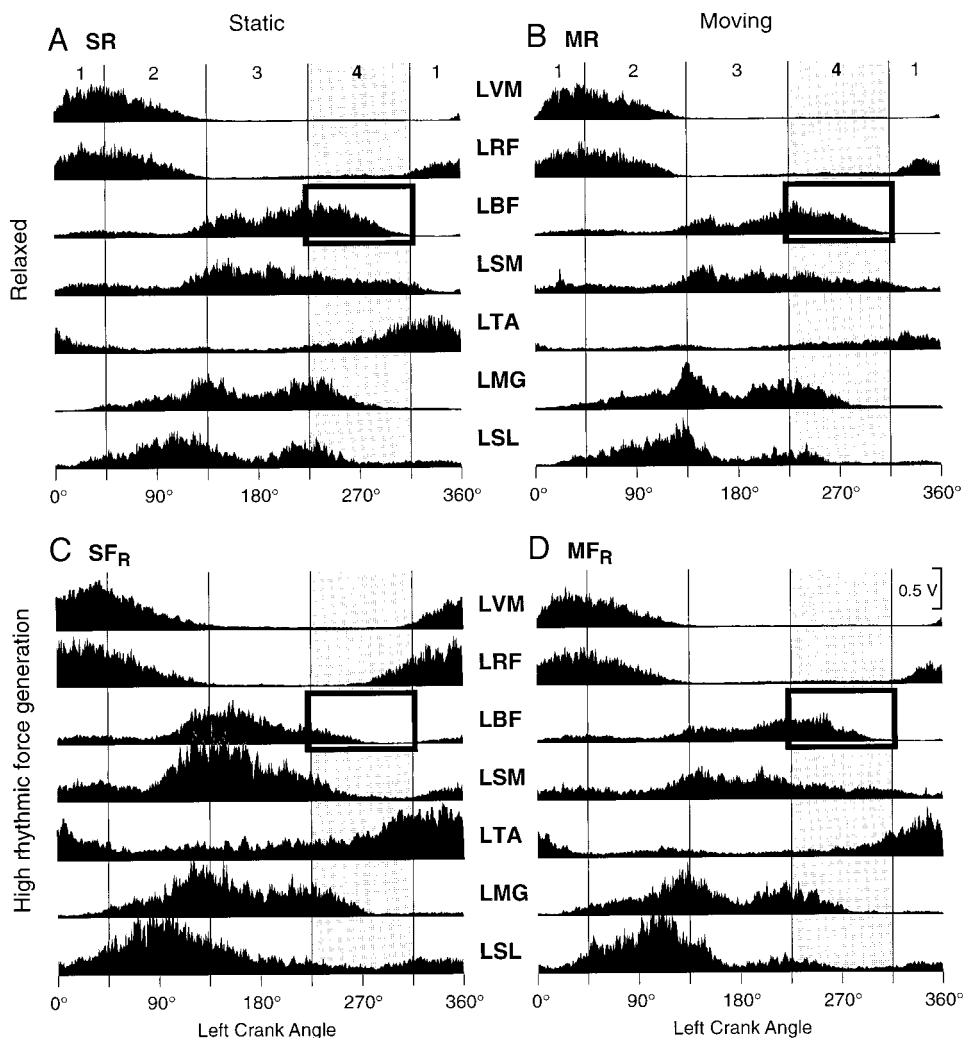


FIG. 7. Electromyograms (EMGs) from 1 subject's pedaling leg (left), averaged over 20 cycles for each of the 4 primary conditions. Activity of left biceps femoris long head (LBF), left semimembranosus (LSM), left rectus femoris (LRF), and left tibialis anterior (LTA) in the flexion-phase (quadrant 4; shading) illustrate the effects of the contralateral, nonpedaling sensorimotor state on pedaling coordination. Flexion-phase activity of LBF is highlighted by a box for comparison. *A*: SR: EMG pattern of 1-legged pedaling with no movement or force generation in the contralateral nonpedaling leg. *B*: MR: EMG activity in quadrant 4 is unaffected by passive movement of the contralateral nonpedaling leg. However, BF activity decreases during the extension-to-flexion transition (quadrant 3). In this subject, though not in general, a decrease in SM and TA activity also occur then. *C*: SF_R: activity of both BF and SM in quadrant 4 decreases with high-force generation in the contralateral, stationary, nonpedaling leg. In this subject, but not in general, TA and RF activity increase. EMG activity also increases during limb extension (quadrant 2). *D*: MF_R: as in SF_R, activity of BF and SM in quadrant 4 decrease when high rhythmic force is generated in the servomoved contralateral nonpedaling leg. MF_R is the only condition where RF and TA activity decrease in quadrant 4 (flexion phase).

muscle activity levels (Fig. 8, A–D, compare SF_T and SF_I with SR; all $P > 0.05$).

Although passive movement of the nonpedaling leg (i.e., MR condition) did not change work output or muscle activity in the pedaling leg during the flexion phase (quadrant 4, see preceding text), BF activity was reduced during the limb extension-to-flexion transition phase [quadrant 3; e.g., compare Fig. 7B (quadrant 3) with Fig. 7A (quadrant 3)]. BF iEMG activity over this transition region when the nonpedaling leg was moved was reduced by 24% compared with the nominal condition when the nonpedaling leg was stationary and resting ($P < 0.01$). The addition of rhythmic high-force generation by the nonpedaling leg (i.e., MF_R condition) had no additional effect on BF activity in quadrant 3 ($P > 0.05$). It should be noted that the limb extension-to-flexion transition (quadrant 3) is a region of the crank cycle where BF is excited in forward two-legged pedaling (Raasch et al. 1997; Ryan and Gregor 1992).

Nonpedaling leg performance

The desired sensorimotor state of the nonpedaling leg was achieved in most conditions as demonstrated by the force and EMG measures. When the nonpedaling leg generated rhythmic force, the force trajectory varied such that there was a single

maximum and minimum per pedaling cycle. The maximum occurred during the flexion phase of the pedaling leg while the minimum occurred during the opposite phase (compare phasing of pedaling leg force in Fig. 9A with phasing of maximum and minimum nonpedaling force peaks in Fig. 9, B and C). The level of extensor force attained and iEMG measured increased with the level of the targeted force. Peak extensor force levels were lowest during the no-force conditions (SR, MR), intermediate during the rhythmic low-force conditions (SF_T, MF_T), and highest during the rhythmic high-force conditions (SF_R, MF_R; compare ▲, ■, and ● in Fig. 9B for maximum extensor force under static conditions, Fig. 9C under movement conditions). Correspondingly, iEMG levels over the crank cycle were higher during high rhythmic force generation (SF_R, MF_R) than during no-force generation (SR, MR; Table 1). Specifically, VM increased almost fourfold, which is significant because it contributes the most to the force and power in limb extension during pedaling (Raasch et al. 1997). In addition to the reduced force observed in the low-force condition, the desired condition of reduced extensor performance was confirmed by iEMG as VM decreased during low- (SF_T, MF_T) compared with high-force generation (SF_R, MF_R; Table 2).

The only desired sensorimotor state not achieved well by the subjects was tonic force generation in their nonpedaling leg

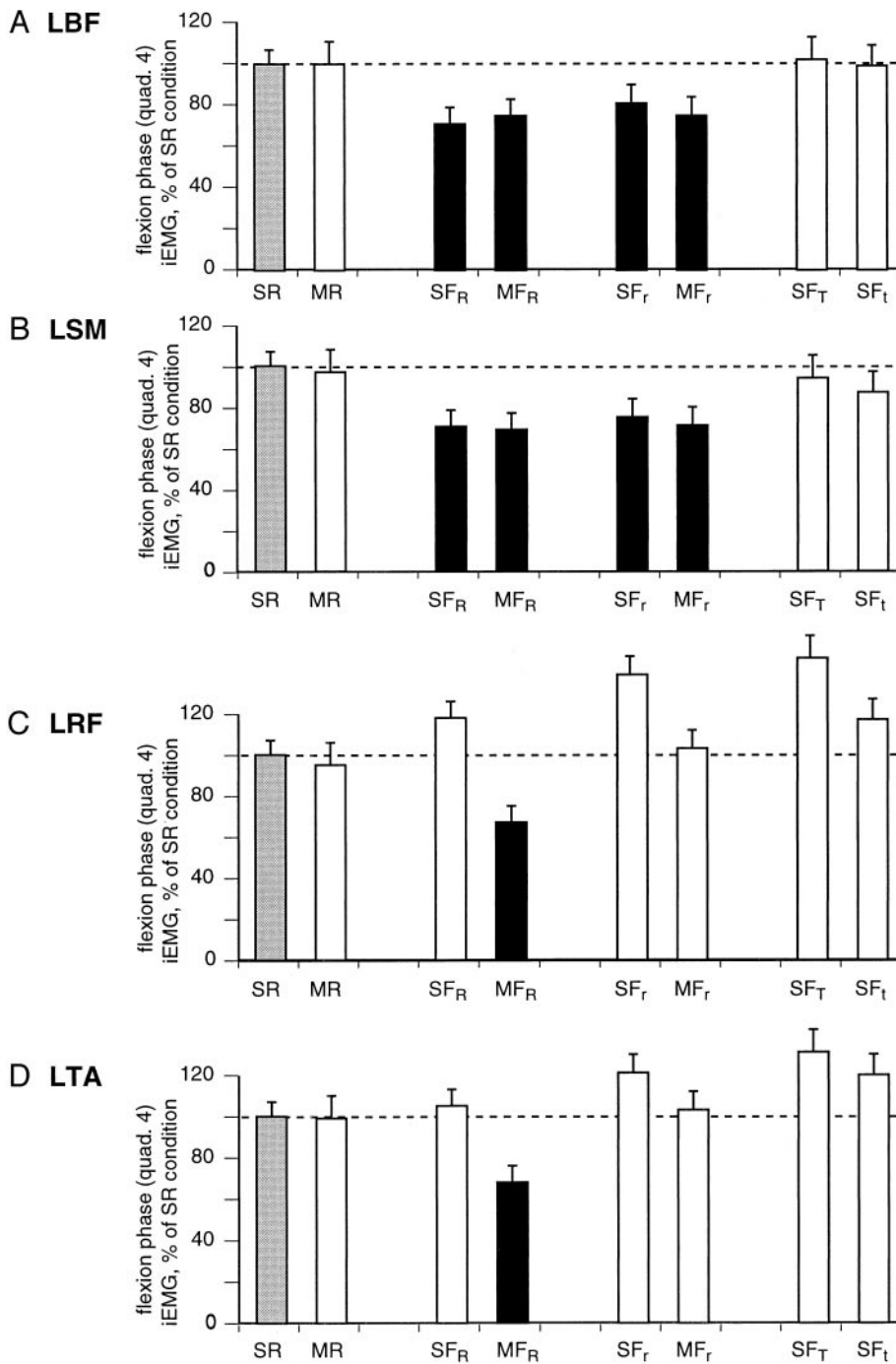


FIG. 8. Integrated EMG (iEMG) from the pedaling leg during the flexion-phase (quadrant 4) as a percentage of iEMG in the nominal (SR) condition, averaged over all subjects. Each muscle shown was predicted to have reduced flexion-phase activity in 2-legged pedaling, compared with 1-legged pedaling with the contralateral nonpedaling leg at rest (Ting et al. 1998b). Bars represent means \pm SE. ---, 100%, the mean activity in the nominal 1-legged condition, SR (\square). A decrease in EMG activity compared with SR is indicated by \blacksquare ($P < 0.01$; except RF activity in MF_R, $P < 0.05$), and represents a change toward 2-legged pedaling coordination. BF (A) and SM (B) activity decrease similarly during high or low rhythmic extensor force generation by the contralateral nonpedaling leg in the presence or absence of being servomoved. RF (C) and TA (D) activity only decrease when high rhythmic extensor force generation in the contralateral nonpedaling leg is accompanied by movement. None of the muscles show a decrease in flexion-phase activity during tonic force generation.

(SF_r, SF_T). Instead of being constant, the extensor force developed in the nonpedaling leg was modulated over the cycle rather than constant (compare \triangle and \square with \blacktriangle and \blacksquare in Fig. 9D). The maximum force produced during the tonic high-force condition (SF_T) was within the bounds of the "high target" region. If a true tonic force had been maintained, the force minima (\triangle and \square , Fig. 9D) would have been equal to the force maxima (\blacktriangle and \blacksquare , Fig. 9D). Although the force minima were significantly lower ($P < 0.01$), the minimum force in the tonic conditions was greater than the minimum force during the rhythmic conditions (compare \triangle and \square in Fig. 9, D with B and C, $P < 0.01$). Thus though substantial extensor force was generated by the nonpedaling leg throughout the cycle in the

tonic force conditions (SF_r, SF_T), this force was phasically modulated, with less force generated when the contralateral pedaling leg was in the extension phase than the flexion phase.

DISCUSSION

Equivalency of task mechanics

Since our experimental conditions were designed to maintain consistent mechanical conditions in the pedaling leg, changes in coordination of the pedaling leg are probably not due to differences in task mechanics or pelvis motion. Pedaling-leg mechanics were highly consistent among cycles be-

cause the torque generated by the constant force spring was very consistent (Fig. 1A). Thus changes in the pedaling performance of subjects could not be due to changes in the mechanical load at the crank (cf. Ting et al. 1998b). Although very little power is normally transmitted through the pelvis in pedaling (Ingen Schenau et al. 1992; Neptune and Hull 1995), energy transfer due to pelvis motion was further minimized by a restraining hip belt. Even though pelvis motion was slightly

TABLE 1. Total *iEMG* comparisons between force-generating and relaxed conditions

Muscle	SF _R /SR	MF _R /MR
RVM	3.73**	3.56**
RRF	1.84**	1.72**
RBF	1.23	1.97**
RSM	1.32	1.29**
RTA	2.64**	2.19**
RMG	1.51	1.48**
RSL	1.60	2.07**

iEMG, integrated electromyogram; RVM, right vastus medialis; RRF, right rectus femoris; RBF, right biceps femoris long head; RSM, right semimembranosus; RTA, right tibialis anterior; RMG, right medial gastrocnemius; RSL, right soleus. SF_R, static force-generating state with a high level of rhythmic force; SR, static relaxed state; MF_R, moving force-generating state with a high level of rhythmic force; MR, moving relaxed state.

** Significant difference from unity at the $P < 0.01$ level.

greater in movement conditions, this did not appear to affect the decrease in flexion-phase crank torque as pelvis motion was not consistently found in either static or movement conditions. Thus the decrease in flexion-phase crank torque was not an artifact of pelvic motion.

Flexion phase pedaling coordination is modulated by contralateral-leg rhythmic extensor force generation

In a previous study, *increased* flexion-phase muscle activity (and *reduced* negative work) compared with bilateral pedaling was measured in subjects pedaling unilaterally with the contralateral leg stationary and relaxed, even though the task mechanics of the pedaling legs were identical in the unilateral and bilateral pedaling conditions (Ting et al. 1998b). Moreover, subjects did not compensate for this increase in muscle activity when given visual feedback of crank torque profile. In our current study, subjects pedaling unilaterally who generated a rhythmic extensor force with their contralateral nonpedaling leg *reduced* the amount of muscle activity (and *increased* the amount of negative work) in the pedaling leg during its flexion

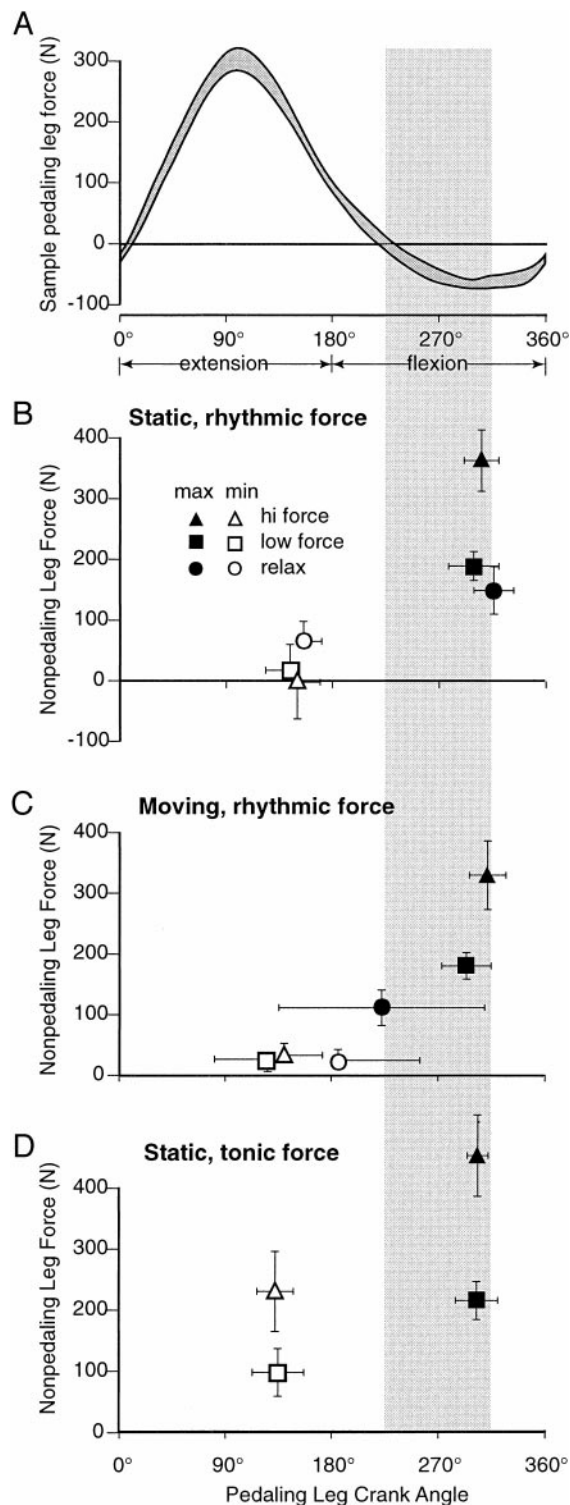


FIG. 9. Maximum and minimum force generated by the nonpedaling leg normal to the pedal and their phasing with respect to the pedaling leg. *A*: force of the pedaling leg normal to the pedal over the crank cycle. *B* and *C*: force of the nonpedaling leg normal to the pedal referenced to the pedaling-leg crank cycle. Positive (extensor) force by either leg indicates a downward force on the pedal, which acts to extend the leg. Extensor force generated by the nonpedaling leg oscillated with a single peak (maximum) and valley (minimum) each pedaling cycle. □, quadrant 4, the mid-flexion region of the pedaling cycle. The phasing and amplitude of the nonpedaling force minima (△, □, and ○) and maxima (▲, ■, and ●) are shown for static, rhythmic force generating conditions of the nonpedaling leg (*B*), for movement and rhythmic force-generating conditions (*C*), and for static, tonic force generating conditions (*D*). The no-force-generating conditions (i.e., “relax”) are also shown in *B* and *C*. Notice that force maxima in all conditions occurred during flexion phase of the pedaling leg, in antiphase with the pedaling leg. Forces were lowest during the no-force-generating conditions (●), intermediate during low-force-generating conditions (■), and highest during high-force-generating conditions (▲). The maximum force during high, rhythmic force generation in both static (▲ in *B*) and movement conditions (▲ in *C*) was comparable to the maximum force generated by the pedaling leg (*A*). During tonic force generation (*D*), the force generated actually oscillated, with maxima significantly greater than minima ($P < 0.01$). Nevertheless, the minimum forces (△ and □) were higher than the minimum forces in the other conditions (e.g., △, □, and ○ in *B* and *C*, $P < 0.01$). The weight of the leg resting on the pedal when the subject was not pedaling ranged from 80 to 130 N.

TABLE 2. Total iEMG comparisons for low and high rhythmic force generation

Muscle	SF _r /SF _R	MF _r /MF _R
RVM	0.43**	0.54**
RRF	0.75	0.81**
RBF	1.31	0.75**
RSM	0.83	0.92
RTA	0.73	0.94
RMG	0.80	0.86
RSL	0.82	0.71**

SF_r and MF_r, static and moving force-generating state with a low level of rhythmic force.

** Significant difference from unity at the $P < 0.01$ level.

phase. The level of reduction of flexion-phase muscle activity also depended on whether contralateral leg movement accompanied the contralateral force generation. Because of major technical limitations in the experimental apparatus at the time, it was impossible for us to include a bilateral pedaling condition; thus we are unable to directly compare the current unilateral pedaling condition (the SR condition) with bilateral pedaling. Nevertheless, the profile of crank torque generation and EMG patterns in the pedaling leg in our current study resemble those of the unilateral pedaling condition in the previous study (Ting et al. 1998b). Thus the mechanisms used by subjects in our current study to reduce flexion-phase muscle activity during contralateral rhythmic extensor force generation may indeed be those involved in the reduction of flexion-phase muscle activity in bilateral pedaling. Regardless, the two studies demonstrate the importance of contralateral sensorimotor state in shaping the default locomotor pattern observed in the flexion phase of pedaling.

Although our current study concentrated on the concurrent effects of contralateral extension on the ipsilateral flexion phase, contralateral force generation appears to affect other phases as well. For example, when the contralateral nonpedaling leg was moved (MR and MF_R conditions), BF activity in the pedaling leg was reduced not only in its flexion phase but also in its extension-to-flexion transition phase. In contrast, when the contralateral leg was stationary and at rest (SR condition), BF activity in the pedaling leg appears to be high not only in its flexion phase (Fig. 8A) but in its extension phase as well. However, the changes that may occur in phases other than flexion (i.e., the extension-to-flexion and flexion-to-extension transition phases, and the extension phase) (Raasch and Zajac 1999; Raasch et al. 1997) cannot be reliably interpreted for the contralateral force generating conditions (cf. contralateral-movement-only condition) because the experimental design did not control the sensorimotor state of the nonpedaling leg well in the other phases. Therefore we have focused on the effects found in the flexion phase of the ipsilateral pedaling leg.

Phase-dependent responses to contralateral sensorimotor state

The different sensitivity of pedaling-leg flexion-phase BF and SM activity and of RF and TA activity to contralateral extensor force generation and movement may reflect their different biomechanical contributions to the execution of pedaling. Computer simulations and experiments of forward and backward pedaling show that BF and SM act primarily to

accelerate the limb posteriorly and RF and TA the limb anteriorly, regardless of pedaling direction (Neptune et al. 2000; Raasch and Zajac 1999; Ting et al. 1999). However, all four muscles (BF, SM, RF, TA) can contribute secondarily to limb flexion (Neptune et al. 2000; Raasch and Zajac 1999; Raasch et al. 1997; Ting et al. 1999), though in different regions of the flexion phase. In forward pedaling, BF and SM contribute to early limb flexion, near the end of their primary contribution to posterior limb movement (e.g., the latter portion of quadrant 3 and the initial portion of quadrant 4; Fig. 3). RF and TA contribute to late limb flexion, near the initial portion of their primary contribution to anterior limb movement (e.g., the latter portion of quadrant 4 and the initial portion of quadrant 1; Fig. 3). Thus the effects of contralateral sensorimotor state on muscles contributing to flexion could reflect a general control strategy for flexors. On the other hand, the effects may depend specifically on each muscle's primary function. Since we were unable to record from iliacus, psoas, and the short head of the biceps femoris, we are unable to assess the contributions from those uniarticular muscles that primarily contribute to limb flexion. Therefore though we hypothesize that uniarticular knee and hip flexor muscles would also show strong influences from contralateral movement and rhythmic force generation, we cannot rule out an alternative hypothesis that only multifunctional muscles contributing secondarily to flexion are affected.

The invariance in level of reduction of flexion-phase BF and SM activity to contralateral sensorimotor state (Fig. 8, A and B: SF_R, MF_R, SF_r, and MF_r conditions) is consistent with a feedforward mechanism based on initiation of force generation in the contralateral leg. Specifically, neither force level nor movement modulated flexion-phase BF and SM activity. Instead, contralateral force generation (both low and high) caused a uniform decrease in flexion phase BF and SM activity in all subjects, regardless of movement condition (Fig. 8, A and B). Since BF and SM activity returns to baseline (Fig. 7) before peak extensor force is generated in the contralateral leg (i.e., before $\sim 315^\circ$ of the pedaling-leg crank angle, Fig. 9, A and B), the magnitude of flexion-phase BF and SM activity may be triggered or programmed by feedforward signals related to initiation of contralateral extensor force rather than modulated by feedback related to contralateral force or movement amplitude. Flexion-phase BF and SM activity may be subject primarily to contralateral feedforward influence because their contribution to propulsion is limited to early flexion phase (Raasch et al. 1997). Similarly, when the leg is obstructed during early swing phase of gait, an invariant muscle coordination pattern emerges; yet when the obstruction occurs in late swing, the pattern is more variable (Eng et al. 1994, 1997). Further, in human locomotion, it appears that flexor activity may be triggered by peripheral input with activity levels modulated by central mechanisms (Dietz 1992). However, there could have been other influences acting on BF and SM activity that were unmeasurable due to the overall low level of EMG activity in BF and SM.

In contrast to BF and SM, flexion-phase RF and TA activity may be influenced by contralateral feedback related to successful generation of both force and movement because the reduction in RF and TA activity only occurred when contralateral force generation accompanied contralateral leg movement, which is the condition (MF_R) studied by us that most replicates

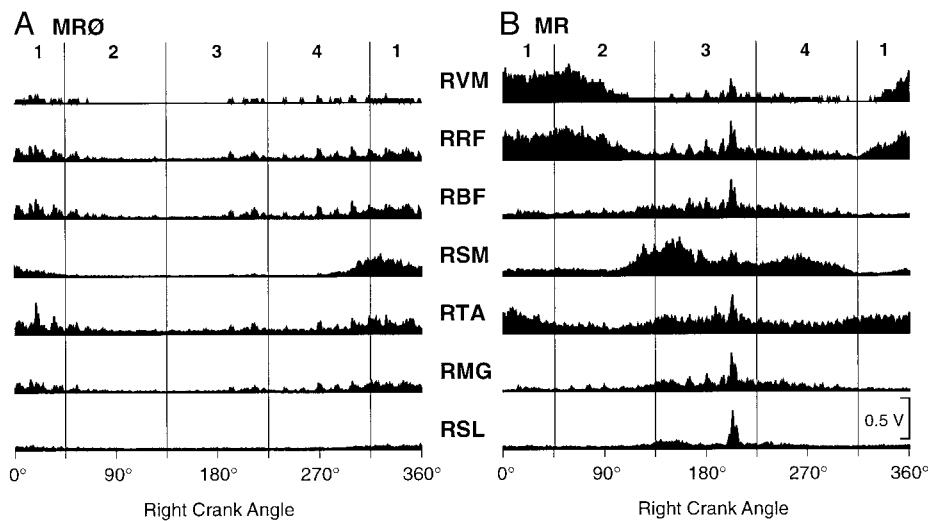


FIG. 10. Average EMG signals from 1 subject's nonpedaling leg (right) when it is relaxed and servomoved. *A*: when the left (usually pedaling) leg is stationary and relaxed, muscles in the right nonpedaling leg are phasically coexcited at the flexion-to-extension transition (quadrant 1), which is unlike the pattern expressed in pedaling (e.g., Fig. 7*D*). *B*: when the left leg pedals, EMG activity in the nonpedaling leg is much higher and patterned as in pedaling. Thus pedaling with only 1 leg (e.g., the left) may excite the 2-legged pedaling generator, causing some or all elements of the pattern to be expressed in the motor output to the nonpedaling leg depending on its excitatory state, which is probably enhanced by ipsilateral (nonpedaling leg) movement (see DISCUSSION). The synchronous bursting in the EMG signals, especially prominent at the extension-to-flexion transition ($\sim 180^\circ$), was seen in a few subjects and is caused by modulated high-frequency motor noise when the motor torque quickly changes. The noise appears in the EMG signals of only the nonpedaling "relaxed" leg because of the low signal-to-noise ratio then (cf. Fig. 7).

two-legged pedaling. Further, high inter- and intra-subject variability of RF and TA activity was found in the force-generating conditions. For example, an *increase* of RF and TA activity, the opposite effect from the norm, was measured in some subjects during isometric force generation (compare LRF and LTA in Fig. 7*C* to LRF and LTA in Fig. 7*A*). Such an increase is consistent with the necessity to excite both contralateral extensors and ipsilateral flexors if contralateral extension alone inadequately propels the crank, such as against very large loads (Raasch et al. 1997). Thus RF and TA activity may be modulated both positively or negatively by contralateral feedback. However, the precise state associated with the successful generation of a high-force and anti-phase movement during contralateral extension appears to cause a decrease in RF and TA activity. Because a precise correlation of RF and TA with force level was not found, RF and TA activity may be affected by other, uncontrolled variables in the experiment. Further, the relatively large range of permissible "high" forces may have contributed to the lack of statistical sensitivity in some conditions.

Neural interlimb coupling constraints on muscle coordination as evidenced by phase-dependent responses to contralateral state appear to reflect functional similarities between ipsilateral flexors and contralateral extensors in two-legged pedaling. In moderate load and steady-state conditions, flexion-phase muscle activity is relatively low while contralateral extensors provide the majority of propulsive power (Kautz and Hull 1993). Although the maximal contribution to propulsion by flexors is small compared with the contribution of extensors, flexors must be recruited nevertheless under high load conditions (Raasch et al. 1997) or when extensors generate inadequate force (e.g., hemiparetic subjects in Kautz and Brown 1998). Thus it is not surprising that a mechanism for activating flexors might exist that is based on contralateral extension that parallels the potential biomechanical contribution of flexors to pedaling. The proposed feedforward and feedback mechanisms would cause flexor activity to increase if either contralateral extension is not initiated or contralateral extension produces inadequate force or movement. Because extrinsic loading in the pedaling leg was constant, contralateral phasic motor commands and dynamic force and movement

feedback signals are possible candidates involved in neural interleg coupling. The neural interleg coupling pathways identified here to be operational during the flexion phase may be indicative of a bilateral recruitment strategy for crank propulsion. However, since activity in uniaxial knee and hip flexors was not measured, the effect may be characteristic of only muscles that act primarily during the limb extension-to-flexion transitions, such as ankle muscles (TA) and biarticular thigh muscles (RF, BF, and SM), that have a secondary contribution to flexion (cf. Cabelguen et al. 1981; Perret and Cabelguen 1980).

One legged pedaling may excite contralateral pattern-generating elements

While the conditions of the nonpedaling leg affect pedaling coordination, conversely, sensorimotor control of one-legged pedaling may provide excitatory drive and modulate pattern-generating elements of the contralateral (nonpedaling) leg. Although the neuronal basis of pedaling coordination is unknown, phasic reflex modulation patterns during pedaling are similar to reflex patterns during walking; thus common neural elements may be employed in pedaling and walking (Brooke et al. 1992–1995, 1997; Collins et al. 1993; McIlroy et al. 1992). In our current study, rhythmic muscle activity patterned as in two-legged pedaling was evoked in the passively moved nonpedaling leg even though subjects were instructed to relax the leg (Fig. 10*B*, MR condition). The phasing of the low-amplitude muscle activity in the "relaxed" nonpedaling leg was similar to the phasing of activity in a leg that actually pedals (compare Fig. 10*B* with Fig. 7*A*). The expression of rhythmic, pedaling-like activity in a nonpedaling leg may depend on the presence of pedaling in the other leg because in the control condition (MRØ), where the ipsilateral (usually pedaling) leg was stationary and relaxed, very little pedaling-like EMG activity was evoked in the contralateral servomoved leg (Fig. 10*A*). The expression of rhythmic, pedaling-like activity in a nonpedaling leg may also require movement because no pedaling-like pattern was evoked in the static, relaxed nonpedaling leg when the other leg pedaled (SR condition) (unpublished nonpedaling-leg EMGs). On the other hand, it is possible that

unilateral pedaling without contralateral movement does indeed excite contralateral pattern generating elements but the expression of the pattern in the motor output is below threshold. Further, the pattern of muscle activity in the nonpedaling leg during the rhythmic extensor force condition (MF_R) was consistent with the extension-phase two-legged pedaling pattern. In contrast, in the absence of pedaling when subjects practiced generating rhythmic force, a nonpedaling-like muscle activity pattern was observed. All of these observations are consistent with bilateral pattern generating elements being excited and modulated even when only one leg pedals, though expression of the pattern in the nonpedaling leg may depend on its sensorimotor state.

The fact that subjects could not produce a constant force with the nonpedaling leg while the other leg pedaled further supports the notion that sensorimotor control of one-legged pedaling excites the pedaling pattern-generating elements of the contralateral leg. Rather than produce a constant force throughout the crank cycle, subjects produced less force in the nonpedaling leg as the pedaling leg executed its extension phase. Generation of the phasic motor output in the nonpedaling leg (evidenced by EMGs as well as force) could be caused by tonic afferent feedback acting to augment the centrally generated locomotor rhythm (review, Rossignol 1996). Phasic motor-output generation in the nonpedaling leg could also be the result of rhythmic inhibition of motoneurons due to activation of spinal locomotor circuits by the other pedaling leg (Orsal et al. 1986) in parallel with tonic supraspinal excitation of the motor pools in the generation of the desired tonic force output. Alternatively, the rhythmic afferent signals from the pedaling leg could have activated interlimb spinal pathways associated with reciprocal inhibition pathways that interact with the tonic supraspinal command at the spinal level (for review, see Jankowska and Edgley 1993). Finally, long-loop sensorimotor pathways could have phasically modulated the descending command (Asanuma and Keller 1991).

Bilateral sensorimotor signals modulate the locomotor pattern

This study provides evidence of modulation of flexor activity in bifunctional muscles by contralateral sensorimotor signals during a steady-state pedaling task. Complex interlimb influences have also been noted in human walking during obstacle avoidance and tripping where only one leg is perturbed (Dietz et al. 1986; Eng et al. 1994). Although neuronal interlimb coordination mechanisms no doubt were present in these studies, the effects due to neural interlimb coupling could not be isolated because of instantaneous mechanical transmission of force to the nonperturbed leg that accompanies contralateral limb acceleration (Yamaguchi and Zajac 1990; Zajac 1993). In our study, mechanical interlimb coupling was almost completely eliminated. Because movement or force generation in one limb did not mechanically affect the other limb, the effect of extension-phase movement and force generation in one leg on flexion-phase EMG patterns in the other leg must be due to neuronal interlimb coupling.

While the basic rhythm and pattern of muscle activity during locomotion may indeed be generated through traditional pattern generation elements, sensory inflow, including motion-dependent, and task-dependent feedback, also affect the rela-

tive timing and duration of muscle activity, as shown in cats (Cabelguen et al. 1981; Smith et al. 1993), chicks (Bekoff et al. 1987), and humans (Andersson et al. 1997). A traditional excitatory connection between contralateral extensor and flexors cannot by itself reproduce the key features of the basic locomotor pattern of flexor bursts being shorter in duration than extensor bursts (cat, Rossignol 1996; chicks, Bekoff et al. 1987) and of the flexor burst period and swing duration changing little with speed while extensor bursts change greatly (cat, Cabelguen et al. 1981; Smith et al. 1993; chick, Bekoff et al. 1987; humans, Andersson et al. 1997; Nilsson et al. 1985). Even in fictive cat preparations, sensory inflow can significantly change the locomotor pattern (Cabelguen et al. 1981; Perret and Cabelguen 1980). In spinal cats, unilateral deafferentation disrupts bilateral pattern generation (Giuliani and Smith 1987). In chicks, bilateral deafferentation of the legs causes flexor activity to increase to nearly the same length as extensor activity (Bekoff et al. 1987), further supporting the concept that sensory information preferentially shapes flexion-phase activity. Finally, the variations in the locomotor pattern observed during different task conditions such as speed and incline (Andersson et al. 1997; Carlson-Kuhta et al. 1998; Nilsson et al. 1985; Pierotti et al. 1989; Smith et al. 1993, 1998) point to the final motor output being shaped by task- and motion-dependent signals to adapt to task demands.

Thus a rich repertoire of task-dependent neuronal interlimb coupling mechanisms, which tend to coordinate the legs as a functional unit, may modulate the basic locomotor pattern during steady-state locomotion and in response to small perturbations. Further, feedforward and feedback mechanisms appear to modulate EMG patterns in pedaling (McIlroy and Brooke 1987) as well as walking (Dietz et al. 1986; Eng et al. 1994), with some EMG patterns changing stereotypically and others in proportion to the stimulus. In addition, these EMG responses vary considerably with task mechanics as well as the phase of the stimulus. For example, the EMG response elicited when the swing leg is impeded by its striking an obstacle (Eng et al. 1994, 1997) differs greatly from the response when the swing leg is impeded by a rope instead (Dietz et al. 1986). In our current study, inadequate force generation in extension by one leg appears to increase flexor force generation in the other leg. Similarly, in hemiplegic chicks, the extension phase of the paretic limb is accompanied by an increased flexion in the contralateral leg, causing an asymmetrical gait pattern (Muir and Steeves 1995; Muir et al. 1998). Thus many interlimb coordination patterns probably exist to coordinate the legs as a functional unit, with the specific set of muscles affected and the intensity of each effect depending on the exact bilateral afferent and efferent state.

Such interlimb coupling mechanisms, which serve to modulate muscle activity during steady-state conditions, may be distinct from the large repertoire of task- and state-dependent interlimb coordination reflexes that reset or interrupt the locomotor rhythm. Studies have demonstrated that stimulation of cutaneous and proprioceptive afferents in various cat preparations prolong and enhance the extension phase and the contralateral flexion phase in a manner similar to that of a Sherringtonian flexion reflex (Duysens and Pearson 1976, 1980; Guertin et al. 1995; Pearson et al. 1992). Further, improper ground support (Gorassini et al. 1994; Hiebert et al. 1994) or stimulation of flexor reflex afferents (Schomburg et al. 1998) in

spinal and intact cats during extension causes a rapid ipsilateral flexion and a contralateral extension. Although such responses do serve to coordinate the legs in a functional manner against large perturbations, they tend to truncate or reset the locomotor rhythm and could be considered separate from the class of interlimb coordination mechanisms demonstrated in our study.

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REFERENCES

- ANDERSSON EA, NILSSON J, AND THORSTENSSON A. Intramuscular EMG from the hip flexor muscles during human locomotion. *Acta Physiol Scand* 161: 361–370, 1997.
- ASANUMA H AND KELLER A. Neuronal mechanisms of motor learning in mammals. *Neuroreport* 2: 217–224, 1991.
- BEKOFF A, NUSBAUM MP, SABICHI AL, AND CLIFFORD M. Neural control of limb coordination. I. Comparison of hatching and walking motor output patterns in normal and deafferented chicks. *J Neurosci* 7: 2320–2330, 1987.
- BERGER W, DIETZ V, AND QUINTERN J. Corrective reactions to stumbling in man: neuronal co-ordination of bilateral leg muscle activity during gait. *J Physiol (Lond)* 357: 109–125, 1984.
- BROOKE JD, CHENG J, COLLINS DF, MCILROY ME, MISIASZEK JE, AND STAINES WR. Sensori-sensory afferent conditioning with leg movement: gain control in spinal reflex and ascending paths. *Prog Neurobiol* 51: 393–421, 1997.
- BROOKE JD, CHENG J, MISIASZEK JE, AND LAFFERTY K. Amplitude modulation of the soleus H reflex in the human during active and passive stepping movements. *J Neurophysiol* 73: 102–111, 1995.
- BROOKE JD, COLLINS DF, AND MCILROY WE. Human locomotor control, the Ia autogenic spinal pathway, and interlimb modulations. In: *Interlimb Coordination: Neural, Dynamical and Cognitive Constraint*. New York: Academic Press, 1994, p. 127–146.
- BROOKE JD, MCILROY WE, AND COLLINS DF. Movement features and H-reflex modulation. I. Pedalling versus matched controls. *Brain Res* 582: 78–84, 1992.
- BROOKE JD, MISIASZEK JE, AND CHENG J. Locomotor-like rotation of either hip or knee inhibits soleus H reflexes in humans. *Somatosens Mot Res* 10: 357–364, 1993.
- BROWN DA AND KUKULKA CG. Human flexor reflex modulation during cycling. *J Neurophysiol* 69: 1212–1224, 1993.
- CABELGUEN JM, ORSAL D, PERRET C, AND ZATTARA M. Central pattern generation of forelimb and hindlimb locomotor activities in the cat. In: *Adv. Physiol. Sci., Regulatory Functions of the CNS. Motion and Organization Principles*, edited by Szentagothai J, Palkovits M, and Hamori J. New York: Pergamon, 1981, p. 199–211.
- CALANCIE B, NEEDHAM-SHROPSHIRE B, JACOBS P, WILLER K, ZYCH G, AND GREEN BA. Involuntary stepping after chronic spinal cord injury. Evidence for a central rhythm generator for locomotion in man. *Brain* 117: 1143–1159, 1994.
- CARLSON-KUHTA P, TRANK TV, AND SMITH JL. Forms of forward quadrupedal locomotion. II. A comparison of posture, hindlimb kinematics, and motor patterns for upslope and level walking. *J Neurophysiol* 79: 1687–1701, 1998.
- COLLINS DF, MCILROY WE, AND BROOKE JD. Contralateral inhibition of soleus H reflexes with different velocities of passive movement of the opposite leg. *Brain Res* 603: 96–101, 1993.
- DIETZ V. Human neuronal control of automatic functional movements: interaction between central programs and afferent input. *Physiol Rev* 72: 33–69, 1992.
- DIETZ V AND BERGER W. Spinal coordination of bilateral leg muscle activity during balancing. *Exp Brain Res* 47: 172–176, 1982.
- DIETZ V, QUINTERN J, BOOS G, AND BERGER W. Obstruction of the swing phase during gait: phase-dependent bilateral leg muscle coordination. *Brain Res* 384: 166–169, 1986.
- DUYSENS J. Reflex control of locomotion as revealed by stimulation of cutaneous afferents in spontaneously walking premaxillary cats. *J Neurophysiol* 40: 737–751, 1977.
- DUYSENS J. A critique of the papers by Rossignol, Julien, Gauthier and Lund; Forssberg; Schomburg, Behrends and Steffens; and Andersson and Grillner. In: *Muscle Receptors and Movement*. London: Macmillan, 1981, p. 433–436.
- DUYSENS J AND PEARSON KG. The role of cutaneous afferents from the distal hindlimb in the regulation of the step cycle of thalamic cats. *Exp Brain Res* 24: 245–255, 1976.
- DUYSENS J AND PEARSON KG. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. *Brain Res* 187: 321–332, 1980.
- ENG JJ, WINTER DA, AND PATLA AE. Strategies for recovery from a trip in early and late swing during human walking. *Exp Brain Res* 102: 339–349, 1994.
- ENG JJ, WINTER DA, AND PATLA AE. Intralimb dynamics simplify reactive control strategies during locomotion. *J Biomech* 30: 581–588, 1997.
- FORSBERG H, GRILLNER S, HALBERTSMA J, AND ROSSIGNOL S. The locomotion of the low spinal cat. II. Interlimb coordination. *Acta Physiol Scand* 108: 283–295, 1980.
- FREGLY BJ AND ZAJAC FE. A state-space analysis of mechanical energy generation, absorption, and transfer during pedaling. *J Biomech* 29: 81–90, 1996.
- GIELEN SC. What does EMG tell us about muscle function? *Motor Control* 3: 9–11, 1999.
- GIULIANI CA AND SMITH JL. Stepping behaviors in chronic spinal cats with one hindlimb deafferented. *J Neurosci* 7: 2537–2546, 1987.
- GORASSINI MA, PROCHAZKA A, HIEBERT GW, AND GAUTHIER MJ. Corrective responses to loss of ground support during walking. I. Intact cats. *J Neurophysiol* 71: 603–610, 1994.
- GRILLNER S. Control of locomotion in bipeds, tetrapods, and fish. In: *Handbook of Physiology. The Nervous System*. Bethesda, MD: Am. Physiol. Soc., 1981, sect. 1, vol. II, p. 1179–1236.
- GRILLNER S AND ROSSIGNOL S. On the initiation of swing phase of locomotion in chronic spinal cats. *Brain Res* 146: 269–277, 1978.
- GRILLNER S AND ZANGGER P. On the central generation of locomotion in the low spinal cat. *Exp Brain Res* 34: 241–261, 1979.
- GUERTIN P, ANGEL MJ, PERREAULT MC, AND MCCREA DA. Ankle extensor group I afferents excite extensors throughout the hindlimb during fictive locomotion in the cat. *J Physiol (Lond)* 487: 197–209, 1995.
- HARKEMA SJ, HURLEY SL, PATEL UK, REQUEJO PS, DOBKIN BH, AND EDGERTON VR. Human lumbosacral spinal cord interprets loading during stepping. *J Neurophysiol* 77: 797–811, 1997.
- HIEBERT GW, GORASSINI MA, JIANG W, PROCHAZKA A, AND PEARSON KG. Corrective responses to loss of ground support during walking. II. Comparison of intact and chronic spinal cats. *J Neurophysiol* 71: 611–622, 1994.
- HOWARD JD AND ENOKA RM. Maximum bilateral contractions are modified by neurally mediated interlimb effects. *J Appl Physiol* 70: 306–316, 1991.
- INGEN SCHENAU GJ v, BOOTS PJ, DE GROOT G, SNACKERS RJ, AND WOENSEL WW v. The constrained control of force and position in multi-joint movements. *Neuroscience* 46: 197–207, 1992.
- JANKOWSKA E AND EDGLEY S. Interactions between pathways controlling posture and gait at the level of spinal interneurons in the cat. *Prog Brain Res* 97: 161–171, 1993.
- KAUTZ S AND BROWN D. Relationships between timing of muscle excitation and impaired motor performance during cyclical lower extremity movement in post-stroke hemiplegia. *Brain* 121: 515–526, 1998.
- KAUTZ SA AND HULL ML. A theoretical basis for interpreting the force applied to the pedal in cycling. *J Biomech* 26: 155–165, 1993.
- MCILROY WE AND BROOKE JD. Response synergies over a single leg when it is perturbed during the complex rhythmic movement of pedalling. *Brain Res* 407: 317–326, 1987.
- MCILROY WE, COLLINS DF, AND BROOKE JD. Movement features and H-reflex modulation. II. Passive rotation, movement velocity and single leg movement. *Brain Res* 582: 85–93, 1992.
- MUIR GD, KATZ SL, GOSLINE JH, AND STEEVES JD. Asymmetric bipedal locomotion—an adaptive response to incomplete spinal injury in the chick. *Exp Brain Res* 122: 275–282, 1998.

- MUIR GD AND STEEVES JD. Phasic cutaneous input facilitates locomotor recovery after incomplete spinal injury in the chick. *J Neurophysiol* 74: 358–368, 1995.
- NEPTUNE RR AND HULL ML. Accuracy assessment of methods for determining hip movement in seated cycling. *J Biomech* 28: 423–437, 1995.
- NEPTUNE RR, KAUTZ SA, AND ZAJAC FE. Muscle contributions of specific biomechanical functions do not change in forward versus backward pedaling. *J Biomech* 33: 155–164, 2000.
- NEWMILLER J, HULL ML, AND ZAJAC FE. 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.
- NORDEEN-SNYDER KS. The effect of bicycle seat height variation upon oxygen consumption and lower limb kinematics. *Med Sci Sports* 9: 113–117, 1977.
- ORSAL D, PERRET C, AND CABELGUEN JM. Evidence of rhythmic inhibitory synaptic influences in hindlimb motoneurons during fictive locomotion in the thalamic cat. *Exp Brain Res* 64: 217–224, 1986.
- PEARSON KG, RAMIREZ JM, AND JIANG W. Entrainment of the locomotor rhythm by group Ib afferents from ankle extensor muscles in spinal cats. *Exp Brain Res* 90: 557–566, 1992.
- PERRET C AND CABELGUEN JM. Main characteristics of the hindlimb locomotor cycle in the decorticate cat with special reference to bifunctional muscles. *Brain Res* 187: 333–352, 1980.
- PIEROZZI DJ, ROY RR, GREGOR RJ, AND EDGERTON VR. Electromyographic activity of cat hindlimb flexors and extensors during locomotion at varying speeds and inclines. *Brain Res* 481: 57–66, 1989.
- 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.
- RAASCH CC. *Coordination of Pedaling: Functional Muscle Groups and Locomotor Strategies* (PhD thesis). Stanford, CA: Stanford University, 1995.
- RAASCH CC AND ZAJAC FE. Locomotor strategy for pedaling: muscle groups and biomechanical functions. *J Neurophysiol* 82: 515–525, 1999.
- RAASCH CC, ZAJAC FE, MA B, AND LEVINE WS. Muscle coordination of maximum-speed pedaling. *J Biomech* 30: 595–602, 1997.
- REDFIELD R AND HULL ML. On the relation between joint moments and pedalling rates at constant power in bicycling. *J Biomech* 19: 317–329, 1986.
- ROSSIGNOL S. Neural control of stereotypic limb movements. In: *Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems*. Washington, DC: Am. Physiol. Soc., 1996, sect. 12, p. 173–216.
- ROSSIGNOL S, CHAU C, BRUNSTEIN E, BELANGER M, BARBEAU H, AND DREW T. Locomotor capacities after complete and partial lesions of the spinal cord. *Acta Neurobiol Exp* 56: 449–463, 1996.
- RYAN MM AND GREGOR RJ. EMG profiles of lower extremity muscles during cycling at constant workload and cadence. *J Electromyogr Kinesiol* 2: 69–80, 1992.
- SCHANTZ PG, MORITANI T, KARLSON E, JOHANSSON E, AND LUNDH A. Maximal voluntary force of bilateral and unilateral leg extension. *Acta Physiol Scand* 136: 185–192, 1989.
- SCHOMBURG ED, BEHRENDTS HB, AND STEFFENS H. Changes in segmental and propriospinal reflex pathways during spinal locomotion. In: *Muscle Receptors and Movement*. London: Macmillan, 1981, p. 413–425.
- SCHOMBURG ED, PETERSEN N, BARAJON I, AND HULTBORN H. Flexor reflex afferents reset the step cycle during fictive locomotion in the cat. *Exp Brain Res* 122: 339–350, 1998.
- SECHER NH, RUBE N, AND ELMERS J. Strength of two- and one-leg extension in man. *Acta Physiol Scand* 134: 333–339, 1988.
- SMITH JL, CARLSON-KUHTA P, AND TRANK TV. Forms of forward quadrupedal locomotion. III. A comparison of posture, hindlimb kinematics, and motor patterns for downslope and level walking. *J Neurophysiol* 79: 1702–1716, 1998.
- SMITH JL, CHUNG SH, AND ZERNICKE RF. Gait-related motor patterns and hindlimb kinetics for the cat trot and gallop. *Exp Brain Res* 94: 308–322, 1993.
- STEIN PSG AND SMITH JL. Neural and biomechanical control strategies for different forms of vertebrate hindlimb motor tasks. In: *Neurons, Network, and Motor Behavior*. Cambridge, MA: MIT Press, 1997, p. 61–74.
- STEIN PSG, VICTOR JC, FIELD EC, AND CURRIE SN. Bilateral control of hindlimb scratching in the spinal turtle: contralateral spinal circuitry contributes to the normal ipsilateral motor pattern of fictive rostral scratching. *J Neurosci* 15: 4343–4355, 1995.
- STEPHENS MJ AND YANG JF. Loading during the stance phase of walking in humans increases the extensor EMG amplitude but does not change the duration of the step cycle. *Exp Brain Res* 124: 363–370, 1999.
- THEEUWEN M, GIELEN CC, AND MILLER LE. The relative activation of muscles during isometric contractions and low-velocity movements against a load. *Exp Brain Res* 101: 493–505, 1994.
- TING LH, KAUTZ SA, BROWN DA, VAN DER LOOS HF, AND ZAJAC FE. Bilateral integration of sensorimotor signals during pedaling. *Ann NY Acad Sci* 860: 513–516, 1998a.
- TING LH, KAUTZ SA, BROWN DA, AND ZAJAC FE. Phase reversal of functional muscle groups in backward human locomotion. *J Neurophysiol* 81: 544–551, 1999.
- TING LH, RAASCH CC, BROWN DA, KAUTZ SA, AND ZAJAC FE. Sensorimotor state of the contralateral leg affects ipsilateral muscle coordination of pedaling. *J Neurophysiol* 80: 1340–1351, 1998b.
- VAN BOLHUIS BM AND GIELEN CC. The relative activation of elbow-flexor muscles in isometric flexion and in flexion/extension movements. *J Biomech* 30: 803–811, 1997.
- YAMAGUCHI GT AND ZAJAC FE. Restoring unassisted natural gait to paraplegics via functional neuromuscular stimulation: a computer simulation study. *IEEE Trans Biomed Eng* 37: 886–902, 1990.
- ZAJAC FE. Muscle coordination of movement: a perspective. *J Biomech* 26 Suppl 1: 109–124, 1993.