

Sensorimotor State of the Contralateral Leg Affects Ipsilateral Muscle Coordination of Pedaling

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¹Rehabilitation R&D Center (153), VA Palo Alto Health Care System, Palo Alto 94304-1200; and ²Mechanical Engineering Department (Biomechanical Engineering Division), and ³Department of Functional Restoration, Stanford University, Stanford, California 94305-3030

Ting, Lena H., Christine C. Raasch, David A. Brown, Steven A. Kautz, and Felix E. Zajac. Sensorimotor state of the contralateral leg affects ipsilateral muscle coordination of pedaling. *J. Neurophysiol.* 80: 1341-1351, 1998. The objective of this study was to determine if independent central pattern generating elements controlling the legs in bipedal and unipedal locomotion is a viable theory for locomotor propulsion in humans. Coordinative coupling of the limbs could then be accomplished through mechanical interactions and ipsilateral feedback control rather than through central interlimb neural pathways. Pedaling was chosen as the locomotor task to study because interlimb mechanics can be significantly altered, as pedaling can be executed with the use of either one leg or two legs (cf. walking) and because the load on the limb can be well-controlled. Subjects pedaled a modified bicycle ergometer in a two-legged (bilateral) and a one-legged (unilateral) pedaling condition. The loading on the leg during unilateral pedaling was designed to be identical to the loading experienced by the leg during bilateral pedaling. This loading was achieved by having a trained human "motor" pedal along with the subject and exert on the opposite crank the torque that the subject's contralateral leg generated in bilateral pedaling. The human "motor" was successful at reproducing each subject's one-leg crank torque. The shape of the motor's torque trajectory was similar to that of subjects, and the amount of work done during extension and flexion was not significantly different. Thus the same muscle coordination pattern would allow subjects to pedal successfully in both the bilateral and unilateral conditions, and the afferent signals from the pedaling leg could be the same for both conditions. Although the overall work done by each leg did not change, an 86% decrease in retarding (negative) crank torque during limb flexion was measured in all 11 subjects during the unilateral condition. This corresponded to an increase in integrated electromyography of tibialis anterior (70%), rectus femoris (43%), and biceps femoris (59%) during flexion. Even given visual torque feedback in the unilateral condition, subjects still showed a 33% decrease in negative torque during flexion. These results are consistent with the existence of an inhibitory pathway from elements controlling extension onto contralateral flexion elements, with the pathway operating during two-legged pedaling but not during one-legged pedaling, in which case flexor activity increases. However, this centrally mediated coupling can be overcome with practice, as the human "motor" was able to effectively match the bilateral crank torque after a longer practice regimen. We conclude that the sensorimotor control of a unipedal task is affected by interlimb neural pathways. Thus a task performed unilaterally is not performed with the same muscle coordination utilized in a bipedal condition, even if such coordination would be equally effective in the execution of the unilateral task.

INTRODUCTION

Spinalized vertebrates and invertebrates use pattern generators and central interlimb coupling mechanisms to coordi-

nate their limbs [for reviews, see Getting (1988), Grillner and Wallén (1985), and Pearson (1993)]. Some evidence exists that humans with spinal cord injuries may also have locomotor pattern-generating capabilities (Calancie et al. 1994; Rossignol et al. 1996). Although studies investigating central interlimb coupling during human lower limb movements showed that perturbations to one leg invoke a coordinated response of the same latency in both legs during stance (Dietz et al. 1989) and locomotion (Berger et al. 1984), the response measured in the contralateral leg may be mediated by changes in sensory input in that leg as a consequence of task mechanics. Because bipedal balance must be maintained, changing the kinematics or kinetics of one leg by perturbation requires a change in loading on the other leg. For example, an antiphase relationship between the legs occurs in human walking even when the left and right belt speeds differ (Dietz et al. 1994). In this situation, lifting one leg because the belt speed is faster on that side will necessarily shift the weight of the subject to the contralateral stance leg or the subject risks falling. Although there may be central interlimb coupling that produces a bilateral response, sensory signals from both legs are also changed from the perturbation itself. Thus interlimb coupling during human walking may arise not only from central interlimb coupling but also from mechanical interlimb coupling that produces bilateral sensory input. In human walking, it is difficult to impossible to separate the two effects.

Clear evidence for central interlimb coupling has nevertheless been demonstrated when the legs participate in a static isometric leg extension task. Force generation by a leg was found to decrease when both legs participated (Howard and Enoka 1991; Schantz et al. 1989; Secher et al. 1988). Because the mechanical conditions imposed on a leg are the same in the unilateral and bilateral isometric tasks, lowered excitation of the muscles during the bilateral task is thought to be centrally mediated.

Ergometer pedaling is ideal for the study of locomotor propulsion because 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. 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. Biomechanical functions and phasing of the muscles appear to be similar during pedaling and walking despite

differences in kinematics (Ting 1998). In both, significant forces are generated and applied to the environment during leg extension phase, whereas in flexion phase much lower forces are applied to the environment, which flex the limb. Although the number of degrees of freedom of movement is greatly reduced because the motion of the feet is constrained to follow the path of the crank in pedaling, simulations show that many different excitation patterns could be used to achieve steady-state pedaling (Raasch 1996). Many biomechanical parameters, such as the load applied to the crank and the phasing between the limbs, can be manipulated as well. Pedaling is therefore an ideal task for studying locomotor mechanisms in humans.

We examined whether the muscle coordination pattern used by one leg during normal two-legged (bilateral) pedaling would also be used in one-legged (unilateral) pedaling, if the loading on the legs were the same in each task. Because the mechanical loading on the legs is the same in both tasks, pedaling coordination can be considered similar if both the net propulsive effect on the crank by muscles during limb extension and flexion (work output) and the excitation pattern of muscles (phasing and amplitude of excitation in extension and flexion) are the same in the two tasks. A previous study of maximum-speed start-up pedaling showed that the excitations of muscles match those predicted by their mechanical function in pedaling (Raasch et al. 1997). Boylls et al. (1984) suggested that muscle coordination in pedaling

could be generated independently in each leg, as electromyographic (EMG) patterns remained coupled with the phase of the ipsilateral leg when interlimb phasing was continuously varied during cranking. Further, studies in insect locomotion showed that coordinated action between the limbs can result through mechanical interactions in the environment alone (Cruse et al. 1998). Thus we hypothesized that pedaling coordination of one leg would be the same in the unilateral and bilateral pedaling conditions.

Normally during pedaling, as in gait, a change in coordination of one limb changes the loading on the other limb (i.e., the load at the crank encountered by the contralateral foot, Fig. 1A). In the experiments to be described, however, a human "motor" assured that the load encountered by the subjects pedaling with one or two legs was the same (Fig. 1B). Because the crank load or environmental influence on pedaling coordination was the same, no mechanical reason existed for subjects to alter their muscle coordination pattern. Thus any change found in coordination pattern would have to be attributed to central rather than mechanical interlimb coupling.

METHODS

Experimental description

A bicycle ergometer was modified such that subjects could pedal with either both legs, as on a standard bicycle ergometer (Fig.

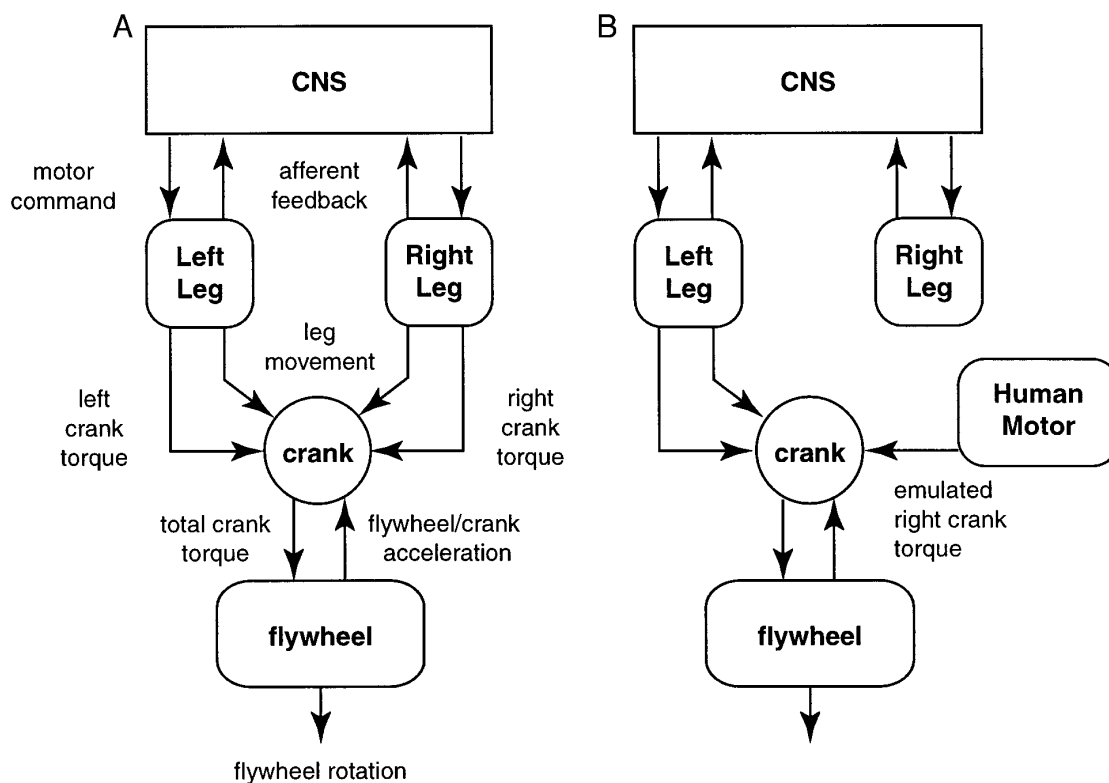


FIG. 1. Schematic diagram of mechanical and neural interactions between left and right legs during seated ergometer pedaling. *A*: mechanical interaction of the legs occurs at the crank, where torque is applied by each leg to accelerate the flywheel. Because the crank is rigid, pushing down faster with one leg will cause the contralateral leg to rise faster, thus altering the afferent feedback from both limbs. *B*: when only the left leg pedals, the mechanics at the crank change dramatically unless the crank torque from the right leg can be externally provided (e.g., by a human "motor"). In this case, mechanics of the pedaling task as experienced by the left leg are the same in the bipedal and unipedal condition. Thus if the right leg does not pedal, it does not alter afferent feedback from the left leg. Therefore any change in coordination of the pedaling leg cannot arise from a change in task mechanics.

2A), or with only one leg while a human “motor” pedaled the opposite crank (Fig. 2B), emulating the mechanical contribution to the crank normally supplied by the subject’s contralateral leg during two-legged (bilateral) pedaling (see DATA PROCESSING for more information about motor training). The motor reliably reproduced the torque trajectory of the contralateral leg of each subject (see RESULTS). Thus the motor generated a large propulsive torque that accelerated the flywheel and assisted leg flexion of the subject’s pedaling leg during the recovery phase, and a small retarding torque that resisted leg extension of the subject’s pedaling leg during the propulsive phase. Thus the resistive and propulsive loads external to the ipsilateral pedaling leg were the same in both the unilateral and bilateral conditions.

The following four conditions were presented in the following order.

Condition 1: bilateral pedaling (Fig. 2A). Subject pedaled normally on the ergometer with both legs.

Condition 2: unilateral pedaling (Fig. 2B). Subjects pedaled with each leg (right and left presented in random order) while the human motor pedaled the opposite crank. The motor used visual torque feedback to match the nominal crank torque trajectory that was generated by the subject’s contralateral leg during bilateral pedaling (condition 1). No feedback was given to the subjects.

Condition 3: unilateral pedaling with feedback (Fig. 2C). Similar to condition 2 (right and left presented in random order), but subjects were also asked to produce, via real-time visual torque feedback, the same one-leg crank torque generated during bilateral pedaling (condition 1).

Condition 4: bilateral pedaling with feedback (Fig. 2D). Subjects pedaled with two legs but were asked to produce, via real-time visual feedback of either the right or left leg crank torque (presented in random order), the same one-leg crank torque generated during bilateral pedaling (condition 1).

The visual torque feedback used by the subjects (conditions 3 and

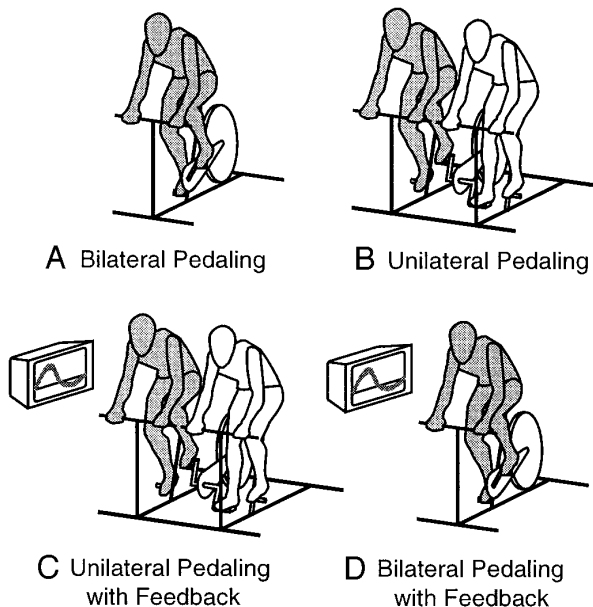


FIG. 2. Four mechanically equivalent pedaling conditions presented to subjects on an ergometer, with a 120 J/cycle frictional workload at 60 rpm. A: bilateral pedaling; standard, 2-legged pedaling. B: unilateral pedaling; 1-legged pedaling that is mechanically similar to bipedal pedaling. A trained human motor (in white) matches the cranking torque normally generated by 1 leg of the subject during the bipedal task. C: unilateral pedaling with feedback; subjects are asked to match the crank torque trajectory (with the use of visual torque feedback) that they generated with 1 leg during bilateral pedaling. D: bilateral pedaling with feedback; subjects pedal bilaterally and are again asked to match the 1 leg torque trajectory from bilateral pedaling.

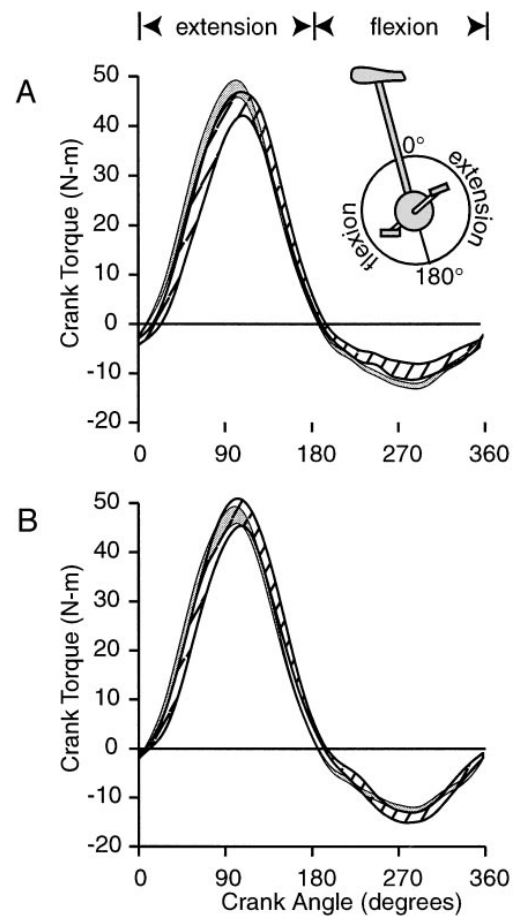


FIG. 3. Example of crank torque trajectory generated by the human motor. Areas indicate ± 1 SD from the mean crank torque. Shaded area represents the crank torque generated by the right leg of the subject during bilateral pedaling, and the hatched area represents the crank torque from the motor emulating the subject’s right leg during (A) unilateral pedaling and (B) unilateral pedaling with feedback. Shape of the motor’s trajectory was similar to that of subjects and did not deviate $>10\%$ from subjects’ mean during upstroke and downstroke. Furthermore, the amount of work done by the motor in upstroke and downstroke was not significantly different from that generated by subjects in bilateral pedaling. Thus the mechanical conditions of the task for the subject’s pedaling leg were similar in both unilateral and bilateral pedaling. In this particular example, the motor generated slightly more downstroke torque than the subject had, which normally causes a more negative upstroke crank torque on the contralateral side. However, as seen in Fig. 4, A and B, upstroke crank torque of the subject was still less negative rather than more negative. A, inset: crank angles are referenced to the ergometer seat tube, which was inclined 73° from horizontal. Leg extension (extension) is between 0 and 180° ; leg flexion (flexion) is between 180 and 360° .

4) and the motor (conditions 2 and 3) consisted of a monitor with a template delimiting ± 2 SDs from each subject’s mean one-leg crank torque trajectory (left-right averaged) during bilateral pedaling (condition 1). Because only subtle differences between left and right torque trajectories were found, the left-right average was used so the same template could be used throughout each session. A filled circle moved horizontally across the screen as a function of crank angle and vertically in proportion to the crank torque generated by the leg. The subjects were asked to perform a visual tracking task, keeping the circle within the boundaries of the template.

In each trial, subjects pedaled at 60 rpm with the use of a metronome. The ergometer seat tube was inclined 73° from horizontal (Fig. 3, inset) and was set to a workload of 120 J/cycle. Subjects wore cleated cycling shoes and pedaled while leaning forward and grasping the handlebars. Subjects were instructed to remain seated

during all trials to minimize movement of the arms and trunk. Subjects were asked to pedal "consistently" for a 40-s trial, with data collected during the last 20 s.

Eleven healthy subjects (8 male, 3 female; age 24 ± 3 yr,

mean \pm SD; height 1.77 ± 0.07 m; weight 69 ± 6 kg) took part in this study. Subjects were not experienced cyclists. None ever rode a bicycle more than 50 miles/wk. Subjects were naive to the experimental goals. All subjects were right dominant for both hand and foot tasks (writing and kicking a ball). This study was approved by the Institutional Review Board (Medical Committee for the Protection of Human Subjects in Research) at Stanford University. Each subject signed a consent form before participating in the study.

Data processing

Normal and shear pedal reaction force, crank and pedal angles, and EMGs from five muscles per leg were collected (see Brown et al. 1996; Raasch et al. 1997). Surface EMGs were measured from the rectus femoris (RF), vastus medialis (VM), biceps femoris long head (BF), tibialis anterior (TA), and medial gastrocnemius (MG) of each leg.

Crank torque produced by each leg, (i.e., the product of the perpendicular component of pedal force that accelerates the crank and crank arm length) was calculated from force and angle data. In any region in the crank cycle, the work done by the leg is directly proportional to the average crank torque. Because the crank torque typically consists of a large positive (propulsive) peak during extension and a negative (resistive) peak during recovery (e.g., Fig. 3), work done in two distinct regions was calculated. Work done by each leg during propulsion (W_p) was calculated between crank angles of 17 and 187° (Fig. 5, inset, W_p), a region in which all subjects generated only positive torque during bilateral pedaling. Work done during recovery (W_r) was calculated in a smaller region between crank angles of 242 and 332° (Fig. 5, inset, W_r), a region in which all subjects generated only negative work during bilateral pedaling. Because timing of transitions from positive to negative torque generation varied among subjects during bilateral pedaling, asymmetry in the regions, with each region defined to be $<180^\circ$, was chosen so errors introduced by including transition regions would be reduced. In general, the amount of work done during the excluded transition regions was $<1\%$ of the total workload and was not different across conditions. The total workload of each trial was calculated by summing the total work done by both legs over the whole cycle (including transition regions). For each trial, all values were calculated by ensemble averaging over 15 crank cycles.

EMG signals were sampled at 1,000 Hz, demeaned, and rectified. As in other pedaling studies, each muscle exhibited one major burst of excitation per cycle (Jorge and Hull 1986; Ryan and Gregor 1992). Thus EMG bursts were characterized by onset angle and offset angle. Muscle bursts were identified by an analysis program that used a threshold activity level of at least $+3$ SD above mean resting EMG levels, a minimum burst duration of 30 ms, and a minimum off period of 40 ms. Each record was visually inspected and edited by hand if necessary to remove spurious bursts and to ensure that the representative burst in each cycle was properly recorded. For each trial, average EMG onset and offset angles from each muscle were found. Mean EMG amplitude over each burst was also calculated.

EMGs were smoothed with a 10-ms moving average, interpolated to 1° crank intervals, and ensemble averaged over 15 crank cycles. The crank cycle was divided into quadrants (Brown et al. 1997) starting from 0° , when the crank is in the upper position aligned with the seatpost (Fig. 7). Thus a crank angle of 0° always corresponds to maximum leg flexion, regardless of seatpost angle (cf. recumbent pedaling), and 180° to maximum leg extension (Brown et al. 1996; Raasch 1996). EMG integrated (iEMG) over each of the four crank cycle quadrants was calculated.

Work, EMG onset, EMG offset, EMG burst amplitude, and quadrant iEMGs were analyzed as a function of pedaling condition with the use of a two-way analysis of variance with subject and leg (nested within subject) as blocking factors. The Student-

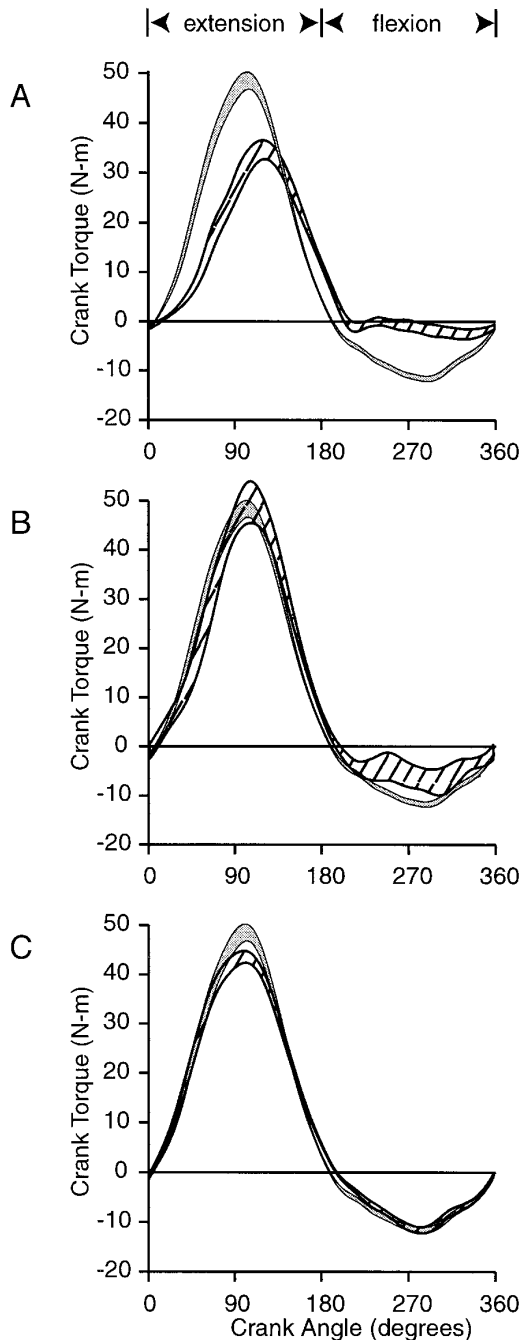


FIG. 4. One leg crank torque during mechanically equivalent conditions for subject JJ, right leg. Shaded areas represents the crank torque ± 1 SD generated by the right leg during bilateral pedaling, and the hatched area represents the crank torque from the right leg during the following conditions. A: unilateral pedaling. Crank torque during upstroke is significantly less negative ($P < 0.01$) in all subjects. Downstroke torque is lower for subject JJ but not for all subjects. B: unilateral pedaling with feedback. Subjects are able to match the crank torque during downstroke. During upstroke, crank torque was intermediate to that of the unilateral and bilateral pedaling and significantly different from both ($P < 0.01$). Note that the width of the shaded area indicates an increase in variability in crank torque generation in upstroke. C: bilateral pedaling with feedback. Trajectories from the 2 bilateral pedaling conditions are similar, indicating no gross effect of performance feedback on the basic pedaling pattern.

TABLE 1. *Recovery phase work (J)*

Subject	Bilateral	Unilateral	Unilateral w/ Feedback	Bilateral w/ Feedback
1	-16.0 ± 1.0	-1.6 ± 1.8	-11.1 ± 3.7	-15.6 ± 1.0
2	-13.9 ± 0.6	-4.9 ± 2.7	-11.6 ± 2.3	-14.4 ± 1.8
3	-12.8 ± 1.2	-2.2 ± 2.7	-7.9 ± 4.1	-14.1 ± 2.5
4	-12.6 ± 1.5	-0.3 ± 2.7	-9.3 ± 3.3	-11.4 ± 2.0
5	-11.5 ± 1.8	-6.7 ± 1.6	-11.0 ± 2.2	-13.1 ± 2.4
6	-9.9 ± 1.7	-2.1 ± 1.5	-6.5 ± 3.2	-11.8 ± 1.7
7	-9.0 ± 1.3	0.7 ± 1.5	-3.5 ± 2.6	-9.2 ± 1.4
8	-7.9 ± 2.8	-2.4 ± 1.9	-7.6 ± 3.7	-11.0 ± 2.9
9	-7.2 ± 1.8	1.4 ± 2.5	-6.4 ± 1.9	-10.9 ± 1.8
10	-6.6 ± 1.6	4.8 ± 4.2	-0.8 ± 2.6	-9.2 ± 2.3
11	-6.5 ± 6.5	-0.3 ± 1.9	-5.1 ± 4.0	-8.3 ± 2.1
Total	-10.4 ± 3.2	-3.1 ± 3.0	-7.3 ± 3.4	-11.7 ± 2.3

Neuman-Keuls post hoc test was applied at a significance level of $P < 0.01$ to test multiple pairwise comparisons between the four conditions.

Human motor training

The human motor was trained over several weeks to match the crank torque trajectories of both the right and left legs of various individuals. The motor practiced daily for ~2 wk in 15- to 30-min sessions, pedaling with lab personnel who purposely tried to vary their pedaling performance. The motor initially had difficulty matching the recovery torque trajectory, but easily matched the propulsive torque trajectory. By the end of the first session, the motor was able to match the negative crank torque in recovery but "with considerable mental effort." Next, during pilot experiments over 4 wk and involving seven individuals, the motor's ability to generate negative recovery torque after a few practice cycles when given visual torque feedback increased. For the 11 subjects of this study, the motor was able to generate negative crank torque without practice, although it was necessary to use the feedback to precisely match each subject's trajectory.

RESULTS

Equivalency of task mechanics

The task mechanics did not change significantly across the trial conditions. The average cadence over all subjects and all trials was 60 ± 2 rpm. The standard deviation in cadence for each subject ranged from 0.1 to 2 rpm, and cadence was not significantly different in any of the pedaling conditions ($P > 0.05$ for all pairwise comparisons). The average frictional workload was 121 ± 5 (SD) J and did not vary by $>5\%$ of mean within each subject's set of trials. However, a time-dependent drift in friction level occurred, such that the workload in the first trial was significantly lower than the last trial by an average of 5 J ($<4\%$ of total workload). Thus work values presented above were normalized for statistical analysis to control for the variation in workload. Subjects remained seated in all conditions, and no difference in pelvis movement in any of the trials was visible in videotapes.

The human motor was able to adequately match the crank torque template (Fig. 3) of each subject as measured by trajectory shape and work done. In the propulsive and recovery regions, the torque trajectories did not deviate from the subject's mean trajectory by more than 10%, indicating that the shape was similar throughout the cycle. Correspondingly, the work done by the motor during either the propulsive or

recovery phase in unilateral pedaling was not significantly different from that generated by the subject during the bilateral condition ($P > 0.05$ for both). Additionally, the total work done by the motor was not significantly different from the work done by one leg of the subject during bilateral pedaling ($P > 0.05$).

Bilateral and unilateral pedaling

During bilateral pedaling, the crank torque and EMGs from one leg were similar to those reported in the literature (Gregor et al. 1991; Ryan and Gregor 1992). The crank torque was negative during recovery (see Fig. 4A, shaded area), as the weight of the leg is propelled by the crank torque generated by the contralateral leg (Kautz and Hull 1993). Thus the large crank torque generated during limb extension, or propulsion (Fig. 4A), serves not only to accelerate the flywheel and overcome the frictional workload but also to raise the contralateral leg in recovery. No differences between the right and left legs were found.

During unilateral pedaling, the crank torque generated by subjects was increased during the recovery phase (e.g., Fig. 4A, Table 1). As a group, subjects generated only 14 ± 30% (SD, $P < 0.01$) of the negative work done by that same leg in bilateral pedaling (Fig. 5A). Some subjects (3/11, Table 1) generated positive work during recovery, indicating muscular effort great enough to overcome the weight of the leg.

Consistent with this increase in crank torque, increased EMG activity in muscles that contribute to flexion was also measured during recovery in unilateral pedaling when compared with bilateral pedaling (e.g., Fig. 6A). In RF and TA, an advance in burst onset during the unilateral condition [by $35 \pm 10^\circ$ (SE) and $54 \pm 20^\circ$ (SE), respectively, $P < 0.01$] corresponds to earlier excitation during the recovery phase (e.g., RF and TA traces in Fig. 6A). BF offset was delayed [$45 \pm 18^\circ$ (SE), $P < 0.01$], corresponding to extended excitation in recovery during unilateral pedaling (e.g., BF trace in Fig. 6A). Correspondingly, iEMG over all subjects was increased during limb flexion in RF, TA, and BF (Fig. 7, quadrants 3 and 4). No significant difference in mean EMG amplitude over the whole burst duration was measured in any of these muscles. No other muscles were found to increase activity during flexion phase (see VM and MG in Fig. 7). It is known from simulations that RF, TA, and BF can each contribute to crank propulsion during flexion phase (Raasch 1996).

A slight decrease in propulsion phase torque during unilateral pedaling compared with bilateral pedaling was found (Fig. 5B). This decrease was not consistent over all subjects (3 subjects generated higher peak forces; 8 generated lower forces). On average, work done in the propulsion phase was $11 \pm 7\%$ (SD) lower in unilateral pedaling than in bilateral pedaling ($P < 0.01$). MG onset was delayed by $17 \pm 6^\circ$ (SE, $P < 0.01$) and VM onset by $11 \pm 6^\circ$ (SE, $P < 0.01$). The only change in iEMG found across all subjects during extension phase was a decrease in MG activity (Fig. 7), which may correspond with the decrease in extensor torque during unilateral pedaling (Fig. 5B).

Pedaling with feedback

When given visual feedback in unilateral pedaling, none of the subjects was able to consistently generate enough

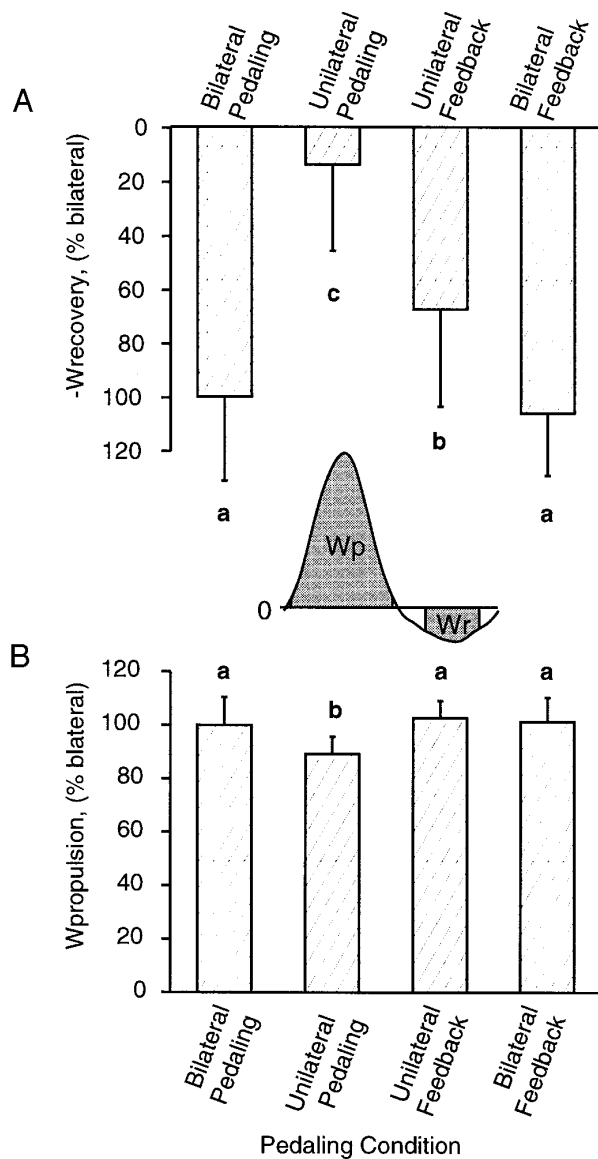


FIG. 5. Normalized upstroke (A) and downstroke (B) work in all conditions compared with bilateral pedaling (mean \pm SD). Upstroke negative work (W_r , inset) is calculated between crank angles of 242 and 332°; downstroke work (W_p , inset) is calculated between 17 and 187°. Letters above/below the bars indicate significantly different groups ($P < 0.01$). A: upstroke. During bilateral pedaling, subjects generated negative crank torque and therefore negative work. In unilateral pedaling, the amount of negative work was $14 \pm 30\%$ of that during bilateral pedaling ($P < 0.01$), with some subjects doing positive work during upstroke. In unilateral pedaling with feedback, subjects generated 67% of the negative work generated during bilateral pedaling ($P < 0.01$). Finally, there was no significant difference between the amount of negative work done in bilateral pedaling with feedback and in the original bilateral pedaling condition ($105 \pm 23\%$, $P > 0.5$). B: downstroke. An average decrease in downstroke work exists during unilateral pedaling compared with bilateral pedaling ($89 \pm 7\%$, $P < 0.01$), but it is small and not apparent in all subjects. No significant differences in downstroke work exist in any of the other conditions.

negative crank torque during recovery to match the torque trajectory generated in bilateral pedaling (e.g., Fig. 4B and Table 1). The average work done during recovery in unilateral pedaling with feedback [i.e., $67 \pm 36\%$ (SD) of the work during bilateral pedaling, Fig. 5A] was intermediate to that of bilateral and unilateral pedaling and significantly different from both ($P < 0.01$). Although the crank torque

trajectories during recovery were more variable during unilateral pedaling with feedback (SD of work done during recovery ranged from 1 to 3.5 times that of bilateral pedaling), they were not statistically different ($P > 0.05$). EMG timing in these trials was also highly variable with no consistent trends across subjects with respect to unilateral pedaling (without feedback). During unilateral pedaling with feedback, work during recovery was not significantly different from the two bilateral pedaling conditions ($P > 0.6$).

In bilateral pedaling with feedback, subjects had little difficulty matching the torque trajectories measured during the original bilateral condition (Fig. 4C). The amount of work during the recovery (Table 1) and propulsion phases were not significantly different from the first bilateral pedaling case ($P > 0.8$ and $P > 0.9$, respectively; Fig. 5). EMG measures were also not significantly different from bilateral pedaling (all $P > 0.05$).

DISCUSSION

Importance of central interlimb coupling

The muscle excitation pattern of a leg during a locomotor task was found to be subject to significant central interlimb coupling because the patterns used in bilateral and unilateral pedaling differed even when the propulsive and resistive forces generated external to the pedaling legs (i.e., the mechanical loading on the legs) remained the same. Ipsilateral muscle coordination during the recovery phase in unilateral pedaling differed from that in bilateral pedaling because retarding crank torque decreased and flexor EMG activity increased. This difference is caused by interlimb neuronal coupling effects, as no change in muscle coordination was warranted by changes in mechanical loading of the legs. Furthermore, the interlimb coupling is substantial because subjects were unable to adequately match the crank torque they generated during bilateral pedaling when they performed unilateral pedaling with feedback. Finally, this centrally mediated coupling can be overcome with practice, as the human motor was able to effectively match the bilateral crank torque after a longer practice regimen.

Constraints on muscle coordination from central interlimb coupling during a human locomotor task have not been previously demonstrated. In fact, muscle activity in each pedaling leg was hypothesized to be generated independently, based on EMG patterns during varying interleg crank-phasing pedaling (Boylls et al. 1984) and H-reflex responses during bilateral pedaling (for review see Brooke et al. 1997). H-reflex modulation in one-legged pedaling indicated that pattern generation of one leg is independent of the other (Brooke et al. 1995; McIlroy et al. 1992).

Equivalency of task mechanics

As in the isometric leg extension experiments (Howard and Enoka 1991; Schantz et al. 1989; Secher et al. 1988), the differences measured here between the bilateral and unilateral pedaling conditions probably cannot be attributed to mechanical factors. The task mechanics for the test leg were tightly controlled to be the same. In each condition, the pedaling leg experienced the same environmental interactions at the seat, or pelvis, and at the pedal. Although some power transfer can occur from linear translation of the hip

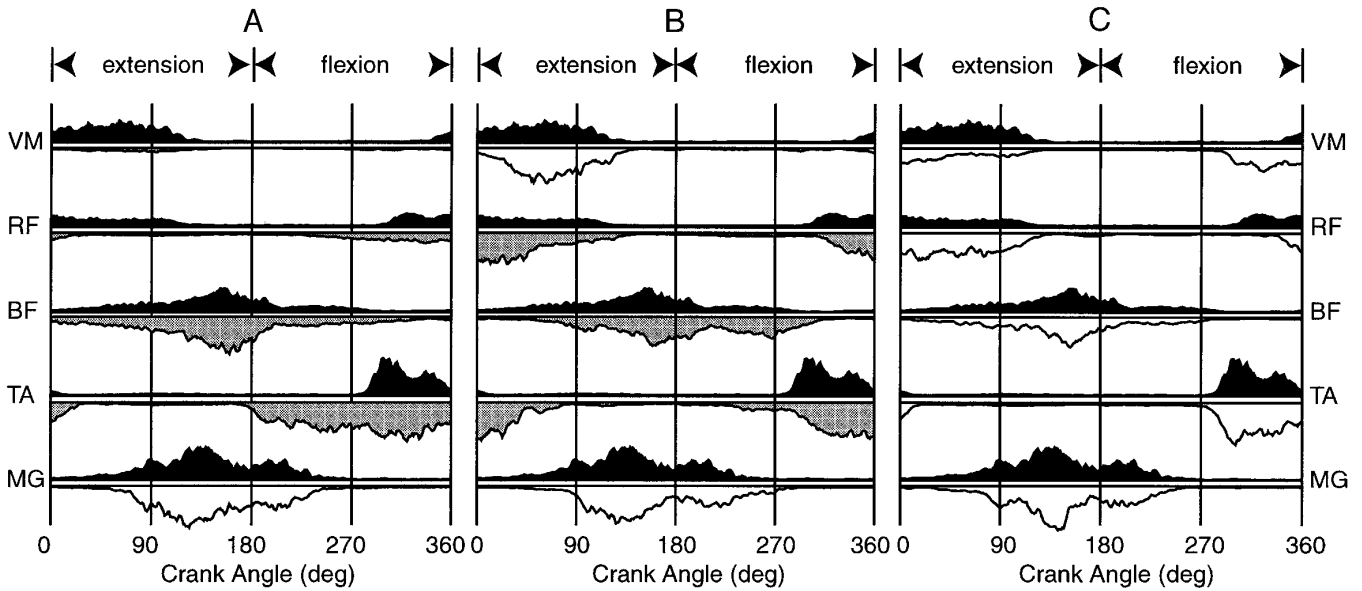


FIG. 6. Averaged electromyographic (EMG) signals from *subject JJ* during mechanically equivalent conditions. Black EMG traces in each plot are identical and correspond to bilateral pedaling. *A*: unilateral pedaling. Vastus medialis (VM) activity is very low, consistent with the subject's low downstroke torque (Fig. 4*A*). EMG activity in upstroke increased in 3 muscles. Rectus femoris (RF) is activated earlier (quadrant 3). Biceps femoris long head (BF) activity is slightly longer, extending into quadrant 4. Tibialis anterior (TA) activity increases greatly in quadrant 3 because of much earlier activation. Medial gastrocnemius (MG) shows little change. *B*: unilateral pedaling with feedback. No common patterns of EMG activity across subjects. VM activity looks similar to that in bilateral pedaling. RF also looks similar; RF amplitude is higher. BF activity is even greater in limb flexion (quadrants 3 and 4) than it was in either bilateral or unilateral pedaling. *C*: bilateral pedaling with feedback. EMGs look similar to that of bilateral pedaling.

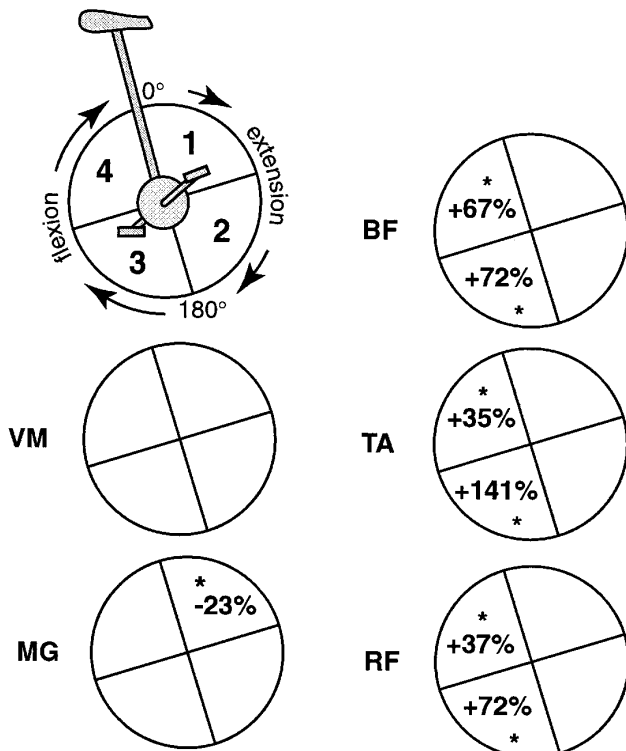


FIG. 7. Integrated EMG (iEMG) per quadrant averaged over all subjects during unilateral pedaling. * Quadrants with significantly greater iEMG with respect to bilateral pedaling ($P < 0.01$). Numbers indicate the percentage increase in iEMG over bilateral pedaling. All iEMG increases occurred during limb flexion in quadrants 3 and 4. This coincides with the decrease in negative crank torque during this region. Decrease in MG activity may contribute to decreased crank torque in limb extension.

during pedaling (Ingen Schenau et al. 1992; Neptune and Hull 1995), this amount is rather small (for 60 rpm, 150 W, total work from hip forces = 4.1 J, with ~0.4 J transmitted during recovery phase) (Neptune and Hull 1995) and could only account for ~5% of the total change in work during recovery (~10 J). Further, videotapes indicated no visible differences in pelvis motion among the conditions, although hip translation was not measured directly. The other environmental interaction was at the crank and consisted of the frictional load as well as the crank torque input provided by the human motor (unilateral pedaling) or the subject's contralateral leg (bilateral pedaling). Because the motor was able to track the crank torque profiles of the subjects, the resistance encountered by the pedaling leg at the crank was the same in all conditions. In fact, the difference observed between unilateral and bilateral pedaling occurred during the recovery phase, which is the phase when the human motor is best able to match the torque that the subjects' contralateral leg would produce had it been pedaling also. Thus the greatest difference in crank torque and EMG activity was observed in a phase where mechanical loading conditions of the task were most similar to those of bilateral pedaling. Finally, impedance properties caused by the inertia of the leg were similar in the bilateral and unilateral conditions, as the supplemental crank torque was supplied by a human leg. We conclude that the mechanics of the pedaling task are the same in all conditions.

Differences between flexion and extension

The increase in TA, RF, and BF activities during limb flexion is consistent with an increased muscle contribution to flexion during recovery. TA is an ankle dorsiflexor that,

by preventing the ankle from collapsing, can help in transmitting to the crank the power generated by hip uniaxial flexors (Fregly and Zajac 1996). Computer simulations also show that higher excitation of TA, RF, and BF (along with iliacus and psoas) during limb flexion increases crank torque in recovery (unpublished observations).

The bias toward increased flexor activity is strong, as subjects cannot reduce it to the level attained in the bilateral condition, even given crank torque feedback. TA, RF, and BF activities during the unilateral condition with feedback were highly variable from subject to subject and often were more active than in all other conditions, indicating that the central bias to excite the flexors is difficult to modify. Subjects often tried to generate negative crank torque by inappropriately exciting other muscles rather than reducing excitation of the flexors, accounting for the inconsistent patterns of muscle excitation observed in unilateral pedaling with feedback.

In contrast, the decrease in crank torque during limb extension in the unilateral condition was probably a compensation for the decrease in negative torque during limb flexion. Because the workload per cycle is constant and the motor performed one-half of the work per cycle, the subject's leg must do one-half of the total workload in each trial. A net increase in recovery phase torque must be compensated by a net decrease in propulsion phase torque, and vice versa, or constant cadence cannot be maintained. Because subjects demonstrated that they could adjust propulsion phase torque easily when given feedback, the decrease in propulsion phase torque is probably not caused by a centrally encoded inhibition of extensors during the unilateral condition. The muscle excitation patterns used in extension seem more modifiable than those of flexion in lower limb tasks (for review see Dietz 1992). Similarly, such differences in reflex responses of extensors and flexors have been observed in several motor tasks (Dietz 1992). Extensor excitation tends to be modulated continuously by peripheral afferent activity, and flexor excitation tends to be triggered by peripheral input and controlled more by central mechanisms.

Organization of the locomotor central pattern generator (CPG)

Conceptually, the spinal locomotor pattern generator has often been hypothesized to be comprised of "half-centers" that control flexors and extensors of each leg (Brown 1914). Because of the flexibility observed in the locomotor pattern, separate locomotor-generating elements for each limb have been hypothesized with interneuronal connections that create coordinated alternation between the limbs [Fig. 8; in humans (Prokop et al. 1995) and in cats (Forssberg et al. 1980); for review see Grillner 1981]. Afferent information has also been shown to be important in modifying and reinforcing spinal pattern generation (for reviews see Andersson and Grillner 1981; Rossignol et al. 1988). Assuming the same interneuronal elements are used in both the unilateral and bilateral conditions, our study examined the nature of the interlimb coupling pathways during pedaling (pathways residing in the CNS of Fig. 1).

One hypothesis compatible with these general concepts of locomotor pattern generation is that the gain of the interneuronal connections between the ipsilateral and contra-

lateral elements is low (Fig. 8, interconnections C). In this case, to pedal in the unilateral condition, the descending command would have to excite only the locomotor elements associated with the pedaling leg (Fig. 8, descending command A). If the muscle excitation pattern should be the same in the two conditions, the afferent feedback signals from the pedaling legs would also be the same because the external loading conditions on the pedaling legs, or task mechanics, are the same. Independent sensorimotor control of each leg could account for the results of Boylls et al. (1984), where muscle excitation in each leg was found to remain phase locked to the ipsilateral leg when interlimb phasing was continuously and predictably varied via a mechanical linkage. However, in our study here, subjects produced active flexion more during the unilateral condition and could not overcome this tendency even when given visual torque feedback. This result is inconsistent with the muscle coordination pattern of a leg being generated without significant contribution from contralateral neural signals.

Thus interconnections between left and right pattern-generating elements must be important to the generation of the pedaling coordination pattern. Perhaps an inhibition of flexor muscles from the sensorimotor control of contralateral limb extension during bilateral pedaling exists (Fig. 8, interconnections C). Because extensor muscles in the nonpedaling leg during unilateral pedaling are inactive, the inhibition

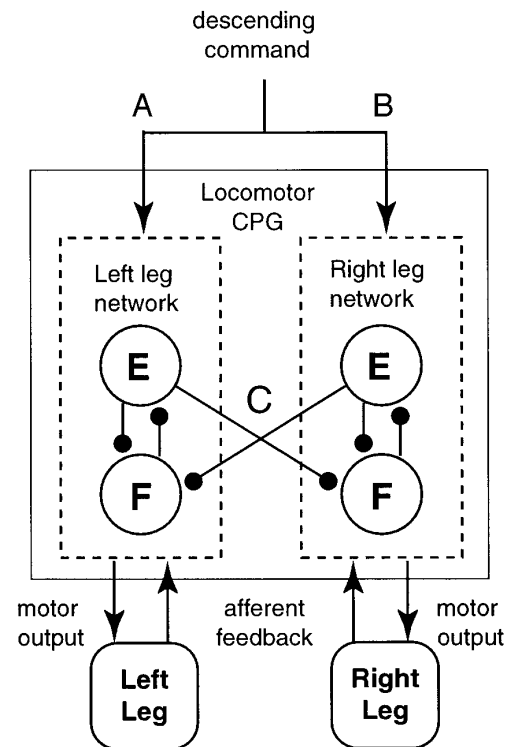


FIG. 8. Proposed interlimb coupling of the locomotor pattern generators, or half-centers. Mutually inhibitory connections between ipsilateral extensors (E) and flexors (F) create alternating flexion and extension of the limb. A and B: parallel descending commands to the left and right limb networks. C: interlimb coupling pathway. If the connections at C have low gain, then ipsilateral muscle coordination patterns would be the same as long as ipsilateral motor command and ipsilateral afferent signals were the same, regardless of contralateral leg movements. An inhibitory connection from E to contralateral F is hypothesized. With only a descending command to the pedaling leg in unilateral pedaling, inhibitory influence from the nonpedaling leg neuronal network is released.

would be released. Such interlimb coupling could be mediated by the flexor reflex pathways (Lundberg 1966; see reviews by Baldissera et al. 1981; McCrea 1992) and is consistent with the mechanics of bilateral pedaling. During bilateral pedaling, flexors contribute little power and do not generate enough crank torque to overcome the weight of the leg in flexion (Hull and Hawkins 1990; Kautz and Hull 1993). Instead, because of mechanical coupling through the crank, the weight of the leg is pushed up by contralateral leg extension. The proposed inhibition of flexors from the sensorimotor control of the contralateral extensors would mean that the power generation in bilateral pedaling would be primarily from extensor muscles, consistent with previous analyses of pedaling (Hull and Hawkins 1990; Raasch et al. 1997).

Gain modulation of afferent pathways

The default strategy during locomotor tasks, such as pedaling and walking, may be to modulate the gain of afferent pathways such that they are strongly effective during limb extension, or the power phase, and ineffective during flexion, or the recovery phase. Prochazka (1989) suggests sensorimotor gain control to be a fundamental strategy employed by the motor system. Also, phase-dependent modulation of reflexes occurs during locomotor tasks. For example, H-reflexes are strongly suppressed during limb flexion in pedaling (Brooke et al. 1992), during the swing phase of walking (Yang and Stein 1990), and in corresponding phases of stepping and passive rotation of the limbs (Brooke et al. 1993, 1995; McIlroy et al. 1992). Similar modulation patterns appear in flexor reflexes (Brown and Kukulka 1993), cutaneous reflexes (Duysens et al. 1990, 1992), and somatosensory evoked potentials during locomotion (for review see Brooke et al. 1997).

Contralateral effects in reflex modulation have also been measured, although H-reflex modulation in a pedaling leg is the same during one- and two-legged pedaling or stepping. H-reflex modulation in the stationary leg during a one-legged pedaling task was demonstrated by McIlroy et al. (1992). Collins et al. (1993) and McIlroy et al. (1992) suggested that contralateral components are not necessary for the single limb to continue undisturbed. However, because the reflex response is already so low during flexion, it may be impossible to measure what appear to be redundant ipsilateral and contralateral sources of reflex inhibition, although both effects can be measured in isolation.

Shared bilateral neuronal circuitry significantly shapes the unilateral pattern

We believe that subjects used the same ipsilateral descending command (Fig. 8, descending command A) to pedal unipedally as bipedally, but the change in sensorimotor state of the nonpedaling leg (e.g., Fig. 1B, right leg) resulted in different motor outputs to the pedaling leg (e.g., Fig. 1B, left leg) because the neuronal circuitry responsible for pedaling is inherently bilateral (cf. "shared bilateral core") (Stein and Smith 1997; Stein et al. 1995). For example, the excitation of an ipsilateral muscle may be strongly influenced by either the excitation of muscles in the contralateral leg or contralateral sensory feedback in addition to ipsilateral com-

mands and sensory feedback. Rossignol (1996) states, "Although each limb can be regarded as an autonomous walking unit, when coupled to the fellow limb, the cycle of the limb is influenced by the cycle of the contralateral limb." We showed that, even when the contralateral sensorimotor state is changed from pedaling to static, muscle coordination of the pedaling leg is altered. Because the control of the legs may be inherently neuronally coupled (e.g., shared bilateral core), muscle coordination of a pedaling leg changes when the other leg no longer pedals. Thus even if the same central command to pedal is used for unilateral and bilateral pedaling, the motor output of a pedaling leg will be appreciably different because contralateral influences on the shared neuronal circuitry are functionally significant. With practice, however, just as interlimb coupling effects can be reduced in the upper limbs (Cohen 1970; Summers and Pressing 1994; Swinnen et al. 1993), our study suggests that coupling effects can be compensated for in the lower limbs because the human motor was able to modify its one-leg crank torque trajectories to match the subjects' when given feedback and extended practice. However, we cannot differentiate whether interlimb coupling gains were modulated with practice with the descending command unaltered or vice versa.

Subjects may use a different strategy to perform the unilateral tasks, which would also account for the differences observed. However, tasks as different as pawshake and locomotion in the cat are probably generated by common neuronal elements (for review see Rossignol 1996). Given the high similarity in unilateral and bilateral pedaling, common neuronal elements are likely utilized to control different pedaling tasks. This is even more likely, given that subjects use the same basic pattern, although computer simulations indicate multiple coordination strategies are possible (Raasch 1996). Nevertheless, even if different elements are used, we would still be able to conclude that a coordination strategy based on knowledge of the mechanics of the ipsilateral pedaling task and ipsilateral afferent feedback information is insufficient to predict muscle coordination. Therefore a strategy based on independent pattern-generating elements for each leg is likewise insufficient to explain pedaling, and probably walking as well, because muscle function and phasing in extensors and flexors during pedaling and walking are similar (Ting 1998).

Conclusions

Our study demonstrates that muscle coordination during pedaling depends on the sensorimotor state of the contralateral leg. Although mechanical cues from the pedaling leg during the unilateral conditions would indicate that the leg could pedal as in the bilateral condition, subjects pedaled as if insufficient crank torque was being generated by the human motor. Thus ipsilateral proprioceptive signals from the leg are insufficient to determine the muscle coordination pattern. In fact, gain modulation of sensory afferent pathways may reduce sensitivity to ipsilateral feedback during limb flexion, which is the phase of the locomotor task found to be most susceptible. These results are consistent with the existence of an inhibitory pathway from elements controlling extension onto contralateral flexion elements, with the pathway operating during two-legged pedaling but not during one-legged pedaling, in which case flexor activity increases.

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