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Journal of Biomechanics 0 (2001) 1–8
JOURNAL
OF
BIOMECHANICS
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Simulation analysis of muscle activity changes with altered body orientations during pedaling

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Accepted 17 January 2000

Abstract

Testing hypotheses related to the effect of gravitational orientation on neural control mechanisms is difficult for most locomotor tasks, like walking, because body orientation with respect to gravity affects both sensorimotor control and task mechanics. To examine the mechanical effect of body orientation independently from changes in workload and posture, Brown et al. J. Biomech. 29 (1996) 1349 studied pedaling at altered body orientations. Brown et al. (1996) found that subjects pedaling at different orientations changed needlessly their muscle excitations, putatively to preserve body-upright pedaling kinematics. We tested the feasibility of this hypothesis using simulations based on a three biomechanical-function pair organization for control of lower limb muscles (limb extension/flexion pair, extension/flexion transition pair, and foot plantarflexion/dorsiflexion pair), where each pair consists of alternating agonistic/antagonistic muscles (Raasch, J. Neurophsiol. 82 (1999) 515. Adjustment of only three parameters, one to scale the muscle excitations of each pair, was sufficient to preserve pedaling kinematics to altered body orientation. Because these adjustments produced changes in muscle excitation and net joint moments similar to those observed in pedaling subjects, the hypothesis is supported. Moreover, the effectiveness of a decoupled gain adjustment procedure where each parameter was adjusted by error in only one aspect of the pedaling trajectory during each iteration (i.e., cadence adjusted the Ext/Flex parameter; peak-to-peak variation in crank velocity over the cycle adjusted the transition parameter; average ankle angle over the cycle adjusted the foot parameter) further supports the distinct function of each muscle pair. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Pedaling; Simulation; Muscle activity; Body orientation; Locomotion

1. Introduction

Testing hypotheses related to the effect of gravitational orientation on neural control mechanisms is difficult in most locomotor tasks, like walking, because task mechanics related to work requirements and body posture change whenever gravity is altered (Carlson-Kuhta et al., 1998; Leroux et al., 1999; Tokuhiro et al., 1985). To examine the mechanical effect of body orientation independently from changes in workload and posture, Brown et al. (1996) studied pedaling at altered body orientations (Fig. 1). Because of the constrained kinematics of pedaling, an invariant net muscle moment pattern at the hip and knee could have been used to pedal regardless of body orientation (Brown et al., 1996). Nevertheless, when body orientation of human subjects was altered, muscle excitations and net muscle moments changed (Brown et al., 1996). Their simulation analysis suggested that changes in the net muscle moments at the hip and knee acted to maintain consistent crank velocity profiles across different body orientations.

Though the simulation analysis of Brown et al. (1996) suggested that changes in net hip and knee moments were needed to maintain a consistent crank trajectory at altered body orientations, certain questions remained unanswered. Because simulations were performed at the joint-torque level without a musculoskeletal model, it could not be demonstrated that the observed changes in muscle excitation were necessitated by the changes in net joint moments. Moreover, EMGs were recorded only from rectus femoris, biceps femoris (long head),

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PII: S0021-9290(01)00014-8

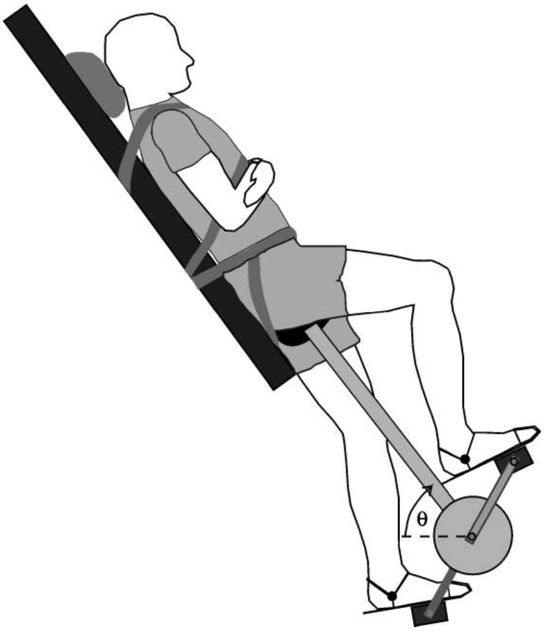

Fig. 1. Experimental setup in Brown et al. (1996) showing the ergometer and subject. θ =tilt angle of backboard, which was used to define body orientation with respect to gravity (horizontal corresponds to 0° and vertical 90°). Figure adapted from Brown et al. (1996).

gastrocnemius, and tibialis anterior, and not from other major contributors to hip and knee moments such as gluteus maximus and vastus medialis. Furthermore, the excitation changes in ankle muscles (gastrocnemius and tibialis anterior) appeared to counteract the effects of gravity on plantarflexion and dorsiflexion (Brown et al., 1996). Thus, it might be reasonable to speculate that ankle muscle excitation maintains proper foot orientation, and hip and knee muscle excitations maintain a consistent crank velocity trajectory. However, this conception may be simplistic because foot orientation affects power transfer to the crank (Raasch and Zajac, 1999), and thus the coordination at the hip and knee is required to maintain a crank velocity trajectory. Finally, the biarticular gastrocnemius muscle, which crosses both the knee and ankle, further complicates the issue of interpreting ankle control independently of hip and knee control.

Forward dynamical simulations are needed to understand task dynamics because the coordination of multijoint movements, like pedaling, is inherently complex, with muscles accelerating both spanned and unspanned joints (Raasch et al., 1997; Zajac, 1993; Zajac and Gordon, 1989). Forward simulations of pedaling to best replicate kinetic and kinematic data have revealed how net joint moments contribute to crank and limb mechanical power (Fregly and Zajac, 1996) and how individual muscles contribute to biomechanical functions during forward and backward pedaling (Neptune et al., 2000). Forward simulations can also be generated to find the muscle coordination that best accomplishes a hypothesized purpose, like maximizing pedaling speed, smoothness, or energy efficiency (Raasch and Zajac, 1999; Raasch et al., 1997). Simulations of the latter give insight into what the nervous system may be trying to accomplish and are useful tools for testing whether a motor control hypothesis is reasonable (Zajac, 1993). In this study, simulations were used to test the feasibility that muscle excitation changes during pedaling at altered body orientations act to maintain a consistent pedaling trajectory (i.e., crank velocity and ankle angle trajectories). Specifically, we propose that the changes in a nominal muscle excitation pattern required to produce a pedaling trajectory invariant to body orientation could reproduce the observed changes in muscle excitation and net joint moments found by Brown et al. (1996). Only three parameters to scale excitations of all the muscles were implemented because an organization of lower limb muscles into three biomechanical-function pairs (limb extension/flexion pair, extension/flexion transition pair, and foot plantarflexion/dorsiflexion pair, where each pair consists of alternating agonistic/antagonistic muscles) seems to be effective for controlling a multitude of pedaling tasks (Neptune et al., 1997, 2000; Raasch and Zajac, 1999; Raasch et al., 1997; Ting et al., 1999).

2. Methods

The planer two-legged pedaling musculoskeletal model developed by Raasch et al. (1997) was used in our simulations (Fig. 2). Briefly, each leg was modeled as three segments with the hip stationary and the foot rigidly attached to the pedal. The two pedals were connected by a crank propelling an "effective" inertial and frictional load (Fregly et al., 2000). The linkage system was driven by 15 musculotendon actuators combined into nine muscle sets with muscles in each set receiving the same excitation signal. Activation (excitation–contraction) dynamics were modeled by first-order differential equations (Raasch et al., 1997). The muscle sets were defined as VAS (three-compartment vastus), GMAX (adductor magnus, gluteus maximus), SOL (soleus, tibialis posterior), PSOAS (iliacus, psoas), BFsh (biceps femoris short head), RF (rectus femoris), HAMS (medial hamstrings, biceps femoris long head), TA (tibialis anterior), and GAS (medial and lateral gastrocnemius). The musculoskeletal geometry and parameters were based on the work by Delp et al. (1990), presently incorporated in SIMM (MusculoGraphics, Inc., Evanston, IL). The dynamical equations-of-motion for the model were generated using SD/FAST (Symbolic Dynamics, Inc., Mountain View, CA).

A "nominal" muscle excitation pattern was derived that, when applied to the pedaling musculoskeletal model, replicated experimental data at the near vertical

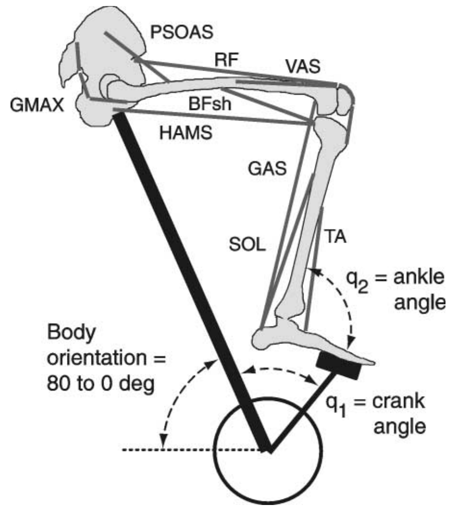

Fig. 2. The planer two-legged pedaling musculoskeletal model developed by Raasch et al. (1997) used in our simulations. The linkage system was driven by 15 musculotendon actuators combined into nine muscle sets. The musculoskeletal geometry and parameters were based on the work by Delp et al. (1990), presently incorporated in SIMM (MusculoGraphics, Inc., Evanston, IL). Body orientation is defined as the angle between the seat tube and horizontal, crank angle between the right crank and seat tube, and ankle angle (right and left) between the foot and shank, as shown. Figure adapted from Neptune and Hull (1998).

body orientation. The near vertical body orientation was chosen to represent nominal pedaling because of its similarity to conventional bicycle and ergometry pedaling. The pedaling data at the most vertical body orientation (i.e., the seat tube inclined 80° from horizontal) of 11 subjects from Brown et al. (1996) were averaged over multiple crank cycles and averaged across subjects while noting intersubject variability. The mean height (176.5 cm) and weight (68.9 kg) of the subjects were close to the representative height ($\sim$180 cm) and weight ($\sim$70 kg) of the musculoskeletal model (Delp et al., 1990).

To judge how well a nominal simulation replicates the pedaling data at the most vertical body orientation (80°), a cost function J was formulated.

$$J = \sum_{j=1}^{m} \sum_{i=1}^{n} \frac{(Y_{ij} - \hat{Y}_{ij})^2}{SD_{ij}^2},$$

where Y_{ij} are the experimentally measured data, $\hat{Y}_{ij}$ are the corresponding simulation data, SD_{ij} are the intersubject standard deviations, n is the number of data points, and m is the number of cost components evaluated (Neptune and Hull, 1998). The cost components included experimental crank torque, net joint torque (at the hip, knee, and ankle), and ankle angle trajectories, as well as onsets and offsets of those muscles where EMGs had been recorded. The onsets and offsets reported by Brown et al. (1996) for tibialis anterior, medial gastrocnemius, rectus femoris, and biceps femoris long head were used to compute the timing errors for TA, GAS, RF, and HAM in the model, respectively. Because EMGs were not available for soleus and vastus medialis (Brown et al., 1996), EMG data from Ting et al. (1999) were used to compute the timing errors for SOL and VAS in the model. All onsets and offsets were weighted equally by the average variability of all onsets and offsets. A cost on cadence error was included to insure that simulations pedaled at close to the experimentally measured cadence of 60 rpm.

To produce the best nominal simulation, a simulated annealing algorithm (Goffe et al., 1994; Neptune, 1999) adjusted 27 controls consisting of the onsets, offsets, and magnitudes of the nine muscle sets, until the cost function J was minimized. Excitation of each muscle set was modeled as a block pattern with lower and upper bounds of 0 and 1, respectively. For the simulation to be consistent with the experimental data, we assumed that all muscles were recruited during the task; thus all muscles were constrained to be on for at least 20% of the crank cycle with a magnitude of at least 5% of maximum. The algorithmic search was stopped when the excitation pattern produced a simulation that tracked each experimental trajectory, and each EMG onset and offset, with an average error that was within one standard deviation of the experimental data.

Next, the nominal excitation pattern associated with a body orientation of 80° was applied to the pedaling model at less-inclined body orientations (60°–0° in 20° increments; Fig. 2) to confirm the suggestion by Brown et al. (1996) that pedaling trajectories at different orientations would differ if the pattern was unchanged. Crank velocity and ankle angle trajectories were compared. To make meaningful kinematic comparisons between body orientations, the excitation magnitudes were all increased or decreased by a small, common percentage to insure that steady-state simulations would have the desired cadence of 60 rpm.

To determine the feasibility that muscle excitation changes during pedaling at less-inclined body orientations may act to maintain a consistent pedaling trajectory, the nominal excitation pattern was modified at each less-inclined body orientation to produce as well as possible the pedaling trajectory associated with the most vertical body orientation (i.e., the crank velocity and ankle angle trajectories at 80°). To accomplish this, three gain parameters, each controlling the excitation magnitude of one of the three biomechanical functional pairs, were adjusted with the simulated annealing algorithm to minimize deviations in pedaling trajectory. Three biomechanical function pairs, where each pair consists of alternating agonistic/antagonistic muscles, have a theoretical basis (Grillner, 1981; Jacobs and Macpherson, 1996; McCollum, 1993; Zajac and Gordon, 1989) and have been used to interpret experimental pedaling data (Neptune et al., 2000; Raasch and Zajac, 1999; Raasch et al., 1997; Ting et al., 1999). The three biomechanical function pairs are the limb extension/flexion pair (representing all uniarticular leg extensors, and flexors except TA), the extension/flexion transition pair (representing the anterior and posterior biarticular thigh muscles), and the foot plantarflexion/dorsiflexion pair (representing the foot dorsiflexors, and plantarflexors except SOL). The nominal excitation magnitudes of all the muscles in a pair were scaled equally (multiplied by the same gain), with the nominal onsets and offsets of the muscles remaining unaltered. Thus, the Ext–Flex gain parameter scaled the excitation magnitude of the uniarticular extensors and flexors (GMAX, VAS, SOL, PSOAS, and BFsh); the transition gain parameter scaled the excitation of the anterior and posterior biarticular thigh muscles (RF and HAMS); and the foot gain parameter scaled the excitation of the plantarflexors (GAS but not SOL; see Discussion), as well as the dorsiflexors (TA) but in the opposite direction (Table 1). A single cost function incorporating three weighted components was minimized. The three components were squared error in cadence (average crank velocity over the crank cycle), squared error in peak-to-peak variation in crank velocity over the cycle, and squared error in ankle angle averaged over the cycle. To reduce errors in both crank velocity variation and ankle angle at less-inclined body orientations (i.e., 60°, 40°, 20°, and 0°), the cost components were weighted to produce equal cost in crank velocity variation and ankle angle error when the nominal pattern pedaled at 0°, the least inclined body orientation (Fig. 2).

Finally, to further confirm the distinct function of each muscle pair, the gain adjustment of each pair was decoupled to reduce error associated with only a single component of the cost function during each iteration. Instead of adjusting the three parameters to minimize a single cost function with three weighted components, cadence error adjusted the Ext-Flex parameter, error in peak-to-peak variation of crank velocity over the cycle adjusted the transition parameter, and error in mean ankle angle over the cycle adjusted the foot parameter (Table 2).

3. Results

The nominal muscle excitation pattern (onset/offset timing and magnitudes) (Fig. 3) found to best replicate the pedaling data at the body inclination of 80° was similar to patterns found in other studies (Neptune and Hull, 1998; Raasch et al., 1997). This pattern produced a nominal pedaling simulation where the average error of each simulated trajectory was within one standard deviation of the experimental trajectory (Fig. 4). However, a sudden increase in hip flexor torque near limb extension (180°) in the simulation was inconsistent with the experimental hip moment [Fig. 4(B)]. The sudden increase in hip flexor torque, also observed in simulations by Neptune et al. (1998), is caused by the sudden onset of PSOAS due its block excitation pattern that does not allow gradual excitation.

When the nominal excitation pattern was applied to the pedaling model at less-inclined body orientations (i.e., 60°, 40°, 20°, and 0°), crank velocity variation remained nearly constant between 80° and 40° of inclination but decreased rapidly from 40° to 0° [Figs. 5(A) and 6(A)]. Ankle angles became more dorsiflexed, reaching a maximum at 20° of inclination [Fig. 6(B)].

Adjustment of the gain parameters (Fig. 7), each of which affects the excitation magnitude of one biomechanical function pair (see above), was able to produce

Table 1
The gain parameters that scaled the nominal excitation magnitudes of muscles grouped into three biomechanical function pairs

Parameter	Description	Muscles
Ext–Flex	Scaled the excitation of all uniarticular extensors (Ext) and flexors (Flex)	Ext: GMAX, VAS, SOL Flex: PSOAS, BFsh
Transition	Scaled the excitation of the anterior (Ant) and posterior (Post) biarticular thigh muscles	Ant: RF Post: HAMS
Foot	Scaled the excitation of the plantarflexors (Plant), as well as the dorsiflexors (Dorsi), but in the opposite direction	Plant: GAS Dorsi: TA

Table 2
Decoupled gain adjustment procedure

Parameter	Gain adjustment procedure
Ext–Flex	If cadence was too slow (fast) in last iteration, increase (decrease) gain by amount proportional to cadence error (from 60 rpm)
Transition	If peak-to-peak variation in crank velocity was too high (low) in last iteration, increase (decrease) gain by amount proportional to error in peak-to-peak variation in crank velocity
Foot	If mean ankle angle was too dorsiflexed (plantarflexed) in last iteration, increase (decrease) excitation of plantarflexors and decrease (increase) excitation of dorsiflexors by amount proportional to error in mean ankle angle

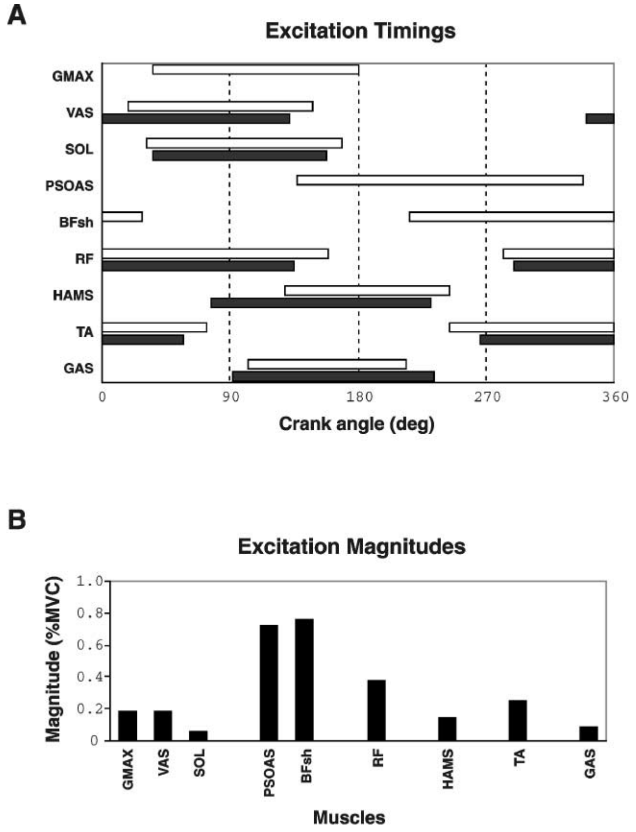

Fig. 3. (A) A comparison of the nominal excitation timing (onset/offset) (white bars) with EMG timing (black bars) (Brown et al., 1996). Notice the good agreement between the simulation-derived muscle excitations and the EMGs. (B) The nominal excitation magnitudes.

simulations at the less-inclined body orientations (i.e., 60°, 40°, 20°, and 0°) with crank velocity variation and ankle angles similar to the nominal simulation (i.e., pedaling at 80° of inclination) [Figs. 5(C), (D) and 6]. At less-inclined body orientations, transition gain decreased much [Fig. 7(B)], Ext–Flex gain increased only slightly [Fig. 7(A)], and plantarflexor and dorsiflexor excitation (controlled by a single foot parameter) increased and decreased much, respectively, reaching a maximum adjustment at 20° of inclination [Figs. 7(C) and (D)]. When each gain parameter was adjusted by errors in only one component of the pedaling trajectory at each iteration in the algorithmic process (i.e., cadence error adjusted the Ext–Flex parameter, error in peak-to-peak variation of crank velocity over the cycle adjusted the transition parameter, and average ankle angle trajectory error adjusted the foot parameter), the final gains found were identical to the gains found when all components had an effect on the adjustment of each gain parameter (Fig. 7).

The muscle excitation changes produced with the adjustments in the three gain parameters agreed qualitatively with the EMG changes observed in subjects pedaling at different body orientations (Brown et al.,

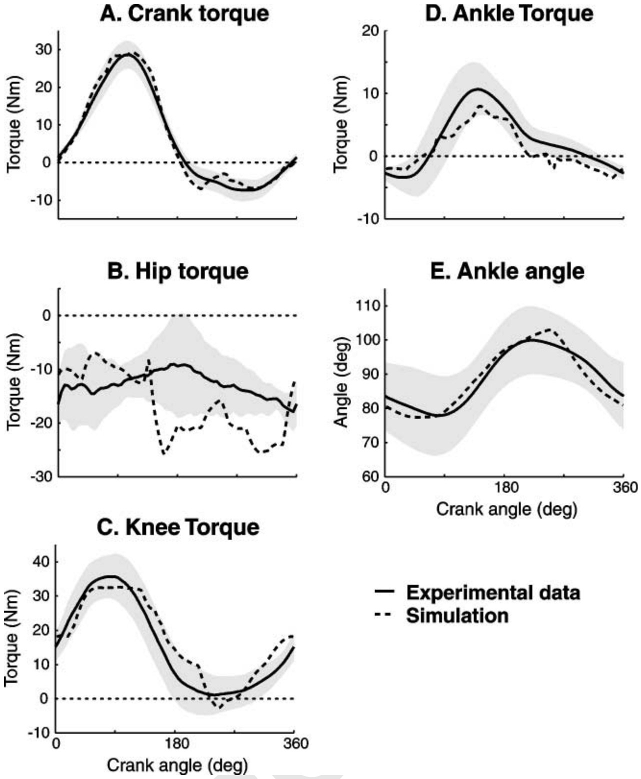

Fig. 4. Comparison of the simulated trajectories (dotted lines) produced by the nominal muscle excitation pattern with the mean experimental trajectories (solid lines) (Brown et al., 1996). Values within plus or minus one standard deviation of the experimental trajectories are represented by the shaded regions. Crank torque is positive in the direction of crank propulsion. Extensor joint torques are represented as positive values. Ankle angle is defined as in Fig. 2. Notice the good agreement between the simulation-derived trajectories and the experimental trajectories, except for the hip torque near 180° (see text).

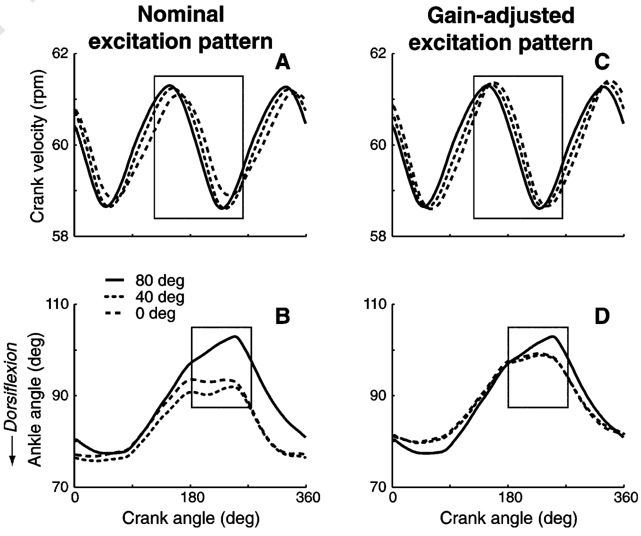

Fig. 5. The pedaling trajectories produced when the nominal [(A) and (B)] and gain-adjusted [(C) and (D)] excitation patterns were applied to the pedaling model at 80°, 40°, and 0° of inclination. Notice the changes in the pedaling trajectory when the nominal excitation pattern was applied and the reduction of these changes when gains were adjusted (highlighted in boxes).

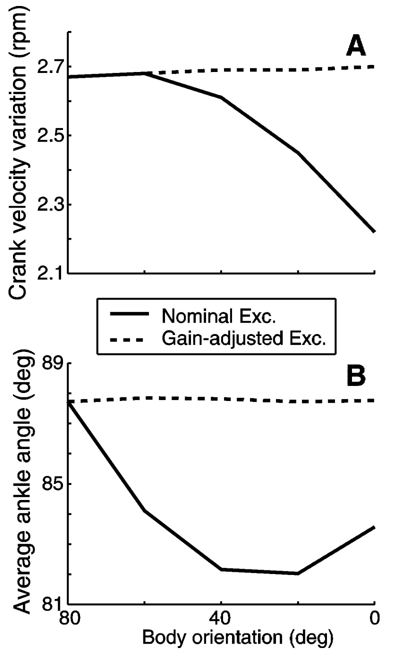

Fig. 6. (A) Peak-to-peak crank velocity variation and (B) average ankle angle produced when the nominal and gain-adjusted muscle excitation patterns were applied to the pedaling model at each body orientation from 80° to 0°. Ankle angle is averaged over the crank cycle. Notice that when the nominal pattern was applied, crank velocity variation was nearly constant between 80° and 40° of inclination but decreased rapidly from 40° to 0°, and maximum dorsiflexion occurred at 20° rather than at 0°, the least inclined body orientation. When the gain-adjusted pattern was applied, crank velocity variation and average ankle angle were nearly invariant across different body orientations.

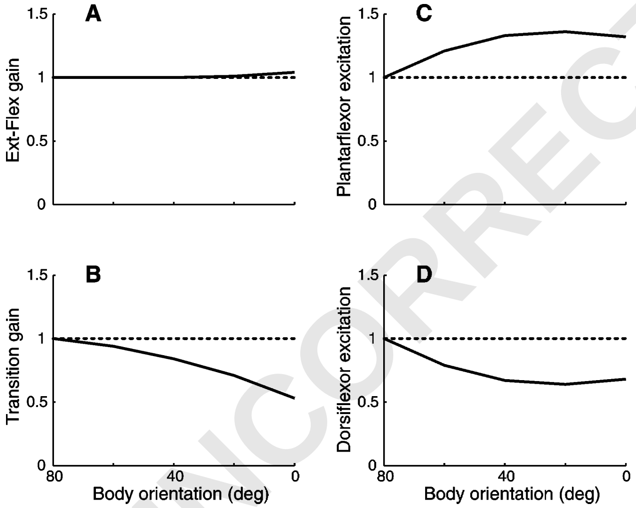

Fig. 7. The adjustments in (A) Ext–Flex and (B) transition gains and (C) plantarflexor and (D) dorsiflexor excitation that were required to produce a pedaling trajectory invariant to body orientation. Plantarflexor and dorsiflexor excitation were controlled by a single foot parameter. At less-inclined body orientations, transition gain decreased much, Ext–Flex gain increased only slightly, and plantarflexor and dorsiflexor excitation increased and decreased much, respectively, reaching a maximum adjustment at 20° of inclination.

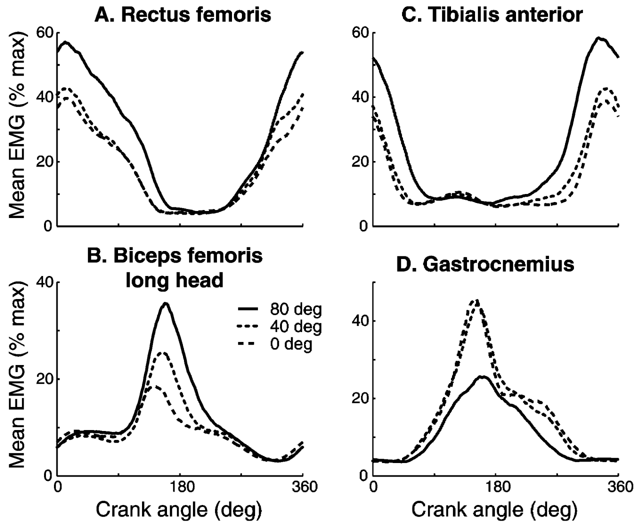

Fig. 8. Experimental EMG data from (A) rectus femoris, (B) biceps femoris long head, (C) tibialis anterior, and (D) gastrocnemius in subjects pedaling at 80°, 40°, and 0° of inclination (Brown et al., 1996). The data were rectified, averaged, smoothed, and normalized to maximum voluntary contractions obtained for each muscle with each subject. EMG activity in rectus femoris and biceps femoris long head decreased at less-inclined body orientations, consistent with similar decreases in transition gain in our simulations. EMG activity in tibialis anterior and medial gastrocnemius decreased and increased, consistent with similar adjustments in foot gain. Figure adapted from Brown et al. (1996).

1996). At less-inclined body orientations, consistent with the decreases in transition gain in our simulations (i.e., in excitation of RF and HAMS by 16% and 47% at 40° and 0° of inclination) [Fig 7(B)], EMG activity in rectus femoris and biceps femoris long head similarly decreased [Figs. 8(A) and (B), 40° and 0°]. Consistent with adjustments in foot gain (by 33% and 32% at 40° and 0° of inclination) [Figs. 7(C) and (D)], EMG activity in tibialis anterior and medial gastrocnemius similarly decreased and increased [Figs. 8(C) and (D), 40° and 0°]. Notice also the similar excitation levels of tibialis anterior at 40° and 0°, and medial gastrocnemius at 40° and 0° [Figs. 8(C) and (D)], consistent with the similar foot gain adjustments at these body orientations [Figs. 7(C) and (D)]. Moreover, gain adjustment of the functional pairs produced systematic changes in the net hip, knee, and ankle joint torques, similar in direction and magnitude to the net joint moment changes observed in pedaling subjects (Brown et al., 1996). At less-inclined body orientations, net hip flexor and knee extensor torque decreased [compare Figs. 9(A) (D) and (B) (E), respectively], and plantarflexor torque increased [compare Figs. 9(C) to (F)].

4. Discussion

Computer simulations based on a three biomechanical-function pair control organization allowed us to

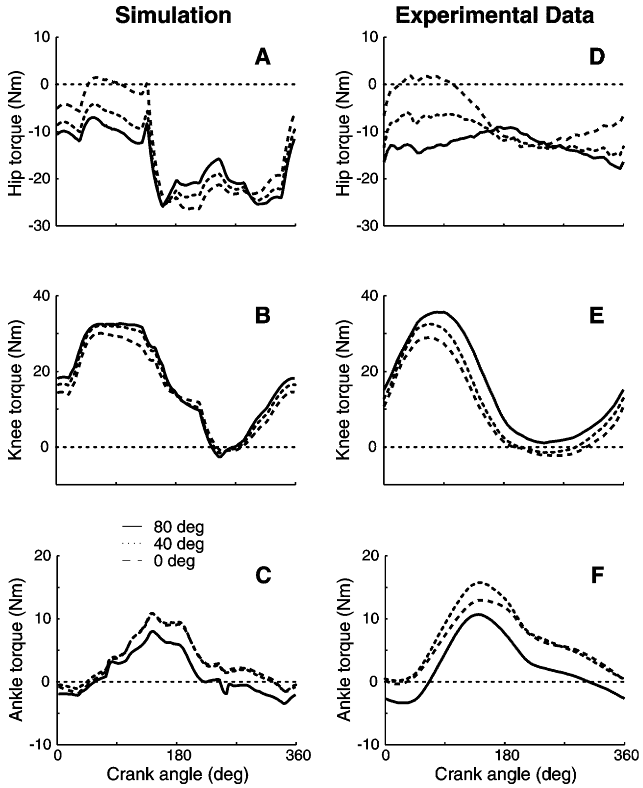

Fig. 9. A comparison of the hip, knee, and ankle torque trajectories [(A), (B), and (C)] produced in simulation at 80°, 40°, and 0° of inclination with the corresponding net muscle moment trajectories [(D), (E), and (F)] produced by pedaling subjects (Brown et al., 1996). Extensor joint torques are represented as positive values. At less-inclined body orientations, hip flexor and knee extensor torque decreased, and plantarflexor torque increased, consistent with similar changes in the experimental net joint moments.

interpret changes in muscle excitation during pedaling at altered body orientations. Gain adjustment of the three parameters controlling the excitation of all the muscles was able to produce a pedaling trajectory invariant to body orientation. The resulting changes in muscle excitation and net joint torques in the simulation at different body orientations agreed with the changes in EMGs and net joint moments observed in pedaling subjects (Brown et al., 1996). Our hypothesis, that changes in excitation act to maintain a consistent pedaling trajectory, was therefore supported.

Although gain parameters were adjusted to produce a pedaling trajectory invariant to body orientation, we do not suggest that humans use pure trajectory control in pedaling; this would imply that any amount of force could be applied to the crank to maintain kinematics precisely. In fact, when human subjects pedaled at different body orientations, crank velocity and ankle angle trajectories changed somewhat (Brown et al., 1996). However, our simulation analyses suggest that trajectory differences would have been greater had subjects not altered their muscle coordination pattern. Thus, at different body orientations, human subjects appeared to use a coordination pattern that was intermediate between a stereotyped nominal pattern and a pattern adjusted to maintain an invariant pedaling trajectory. A coordination pattern with this characteristic is consistent with impedance control where a reference trajectory is commanded and a "disturbance response" is given to deviations from the motion in the form of a stiffness (Hogan, 1985). Impedance control is particularly important in controlling dynamic behavior where power is exchanged between the end-effector and environment (Hogan, 1985), as between the foot and crank in pedaling. Our results, generated with the assumption of trajectory control, are also consistent with impedance control since the direction of muscle excitation changes due to environmental perturbations are expected to be the same for a commanded trajectory, whether impedance or trajectory control is used. However, in impedance control, kinematic trajectories are not maintained precisely when task mechanics are altered.

Because Brown et al. (1996)did not record EMGs from uniarticular leg extensors and flexors, we could not substantiate the changes in the Ext–Flex gain parameter in our simulations. Interestingly, the Ext–Flex parameter was nearly invariant across all body orientations while transition and foot parameters changed much. Because SOL is typically co-active with other leg extensor muscles in pedaling, SOL was classified as a leg extensor in the Ext/Flex pair. However, SOL could have been reasonably classified as a plantarflexor as well since it contributes to both leg extension and plantarflexion in pedaling (Neptune et al., 2000; Raasch et al., 1997; Ting et al., 1999). We generated other simulations with SOL classified as a plantarflexor, and therefore its excitation was adjusted by the foot parameter, and found that pedaling trajectories invariant to body orientation could be achieved equally well. However, in this case, SOL excitation was increased along with the other plantarflexors in contrast to the little change found when SOL was grouped with the leg extensor muscles. Since Brown et al. (1996) did not record EMGs from SOL, we have no basis from this study to classify SOL. However, Neptune et al. (1997) found a coupling between GMAX (an extensor muscle) and SOL EMG activity as they varied in the same non-linear fashion across different pedaling rates while most other muscles varied linearly.

The three biomechanical-function pair control organization allowed the gain adjustment procedure to be simplified so that each parameter was adjusted by error in only one aspect of the pedaling trajectory during each iteration. This further confirms the distinct function of each muscle pair in our control organization and the dominance of each pair over certain aspects of the pedaling trajectory. In essence, gain adjustment of the Ext/Flex pair controlled cadence (or equivalently, power generation to the crank), the transition pair the crank velocity trajectory, and the foot pair the orientation of the foot. The control of cadence by the Ext/Flex pair is consistent with the uniarticular hip and knee extensors generating the majority of the power used to propel the crank in pedaling (Neptune et al., 2000; Raasch et al., 1997). The adjustment of the crank velocity profile by the transition pair is consistent with the view that biarticular muscles serve to fine-tune the coordination of multi-joint lower limb tasks (Zajac, 1993) and, specifically, provide smooth pedaling (Raasch and Zajac, 1999). Moreover, the control of foot orientation by the foot pair is consistent with its role in positioning the foot so that energy is effectively transferred to the crank (Fregly and Zajac, 1996; Fregly et al., 2000; Neptune et al., 2000; Raasch et al., 1997).

In summary, gain adjustment of three biomechanical pairs to produce a pedaling trajectory invariant to body orientation resulted in muscle excitation and joint torque changes at different body orientations that agreed with experimental pedaling data (Brown et al., 1996). The simulation results support our hypothesis that changes in muscle excitation at different body orientations act to maintain a consistent pedaling trajectory. A decoupled gain adjustment procedure where each parameter was adjusted by error in only one aspect of the pedaling trajectory during each iteration converged upon the same parameters as those found by a single cost function with three weighted components. The effectiveness of the decoupled gain adjustment procedure further validates our use of a control organization based on three biomechanical-function pairs in interpreting experimental pedaling data.

Acknowledgements

We thank Christine Raasch for her helpful comments on the simulations, Richard Neptune for his comments on the simulations and for reviewing the manuscript, and David Brown for providing access to the experimental data. This work was supported by a Whitaker Foundation Predoctoral Fellowship, NIH Grant NS17662, and the Rehabilitation R&D Service of the Department of Veterans Affairs (VA).

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