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Muscle contributions to specific biomechanical functions do not change in forward versus backward pedaling

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Abstract

Previous work had identified six biomechanical functions that need to be executed by each limb in order to produce a variety of pedaling tasks. The functions can be organized into three antagonistic pairs: an Ext/Flex pair that accelerates the foot into extension or flexion with respect to the pelvis, an Ant/Post pair that accelerates the foot anteriorly or posteriorly with respect to the pelvis, and a Plant/Dorsi pair that accelerates the foot into plantarflexion or dorsiflexion. Previous analyses of experimental data have inferred that muscles perform the same function during different pedaling tasks (e.g. forward versus backward pedaling) because the EMG timing was similar, but they did not present rigorous biomechanical analyses to assess whether a muscle performed the same biomechanical function, and if so, to what degree. Therefore, the objective of this study was to determine how individual muscles contribute to these biomechanical functions during two different motor tasks, forward and backward pedaling, through a theoretical analysis of experimental data. To achieve this objective, forward and backward pedaling simulations were generated and a mechanical energy analysis was used to examine how muscles generate, absorb or transfer energy to perform the pedaling tasks. The results showed that the muscles contributed to the same primary biomechanical functions in both pedaling directions and that synergistic performance of certain functions effectively accelerated the crank. The gluteus maximus worked synergistically with the soleus, the hip flexors worked synergistically with the tibialis anterior, and the vasti and hamstrings functioned independently to accelerate the crank. The rectus femoris used complex biomechanical mechanisms including negative muscle work to accelerate the crank. The negative muscle work was used to transfer energy generated elsewhere (primarily from other muscles) to the pedal reaction force in order to accelerate the crank. Consistent with experimental data, a phase shift was required from those muscles contributing to the Ant/Post functions as a result of the different limb kinematics between forward and backward pedaling, although they performed the same biomechanical function. The pedaling simulations proved necessary to interpret the experimental data and identify motor control mechanisms used to accomplish specific motor tasks, as the mechanisms were often complex and not always intuitively obvious.

Keywords: Pedaling; Muscle power; Simulation; Motor control; Locomotion

1. Introduction

Studies contrasting forward and backward locomotion in quadrupedal (e.g. Buford and Smith 1990; Grillner 1981) and human (e.g. Grasso et al. 1998; van Deursen et al. 1998) gait have attempted to identify neural control mechanisms that produce the locomotor patterns. However, these studies did not examine the motor patterns using a theoretical framework that included identifying the biomechanical functions executed by individual muscles during performance of the motor task, as well as how these functions may have changed during forward and backward locomotion.

Raasch et al. (1997) were the first to provide a theoretical framework to evaluate a muscle's contribution to the biomechanical functions necessary to satisfy the locomotor task requirements in pedaling. Experimental and theoretical pedaling studies using this framework have identified six biomechanical functions executed by each limb that can be organized into three pairs of alternating

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antagonistic functions capable of producing a variety of pedaling tasks (Raasch and Zajac, 1999; Ting et al., 1999). The pairs were organized into an Ext/Flex pair that accelerates the foot into extension or flexion with respect to the pelvis, an Ant/Post pair that accelerates the foot anteriorly or posteriorly with respect to the pelvis, and a Plant/Dorsi pair that accelerates the foot into plantarflexion or dorsiflexion (Fig. 1). In the context of pedaling, phasing of individual muscle excitations are determined by each muscle's ability to contribute to specific biomechanical functions in order to produce crank acceleration. Some muscles have been shown to be capable of contributing to more than one function (e.g. rectus femoris can contribute to both the Ext and Ant functions in forward pedaling (Raasch et al., 1997)).

Ting et al. (1999) experimentally investigated forward and backward pedaling and concluded that there was a direction-dependent modulation of the muscles contributing to specific biomechanical functions. Based on the work of Raasch and Zajac (1999) they had hypothesized that a phase reversal in the muscles contributing to the Ant/Post pair would be necessary to adapt to the changing task mechanics (i.e. the anterior and posterior motion of the limb occurs at the opposite flexion/extension transitions in backward pedaling, Fig. 1). They had also hypothesized that the muscles contributing to the Ext/Flex and Plant/Dorsi pairs would remain unchanged since those functions remain invariant with pedaling direction. In their EMG data, Ting et al. (1999) observed significant phasing shifts in the muscles predicted to contribute to the Ant/Post functions (although rectus femoris no longer appeared to contribute to the Ant function) and did not observe significant phasing shifts in the muscles predicted to contribute to the Ext/Flex and Plant/Dorsi functions. Thus, the EMG timing data appeared to support the hypothesis that muscles contributed to the same functions in forward and backward pedaling, although some minor differences caused them to suggest that some muscles might also contribute to secondary functions in backward pedaling.

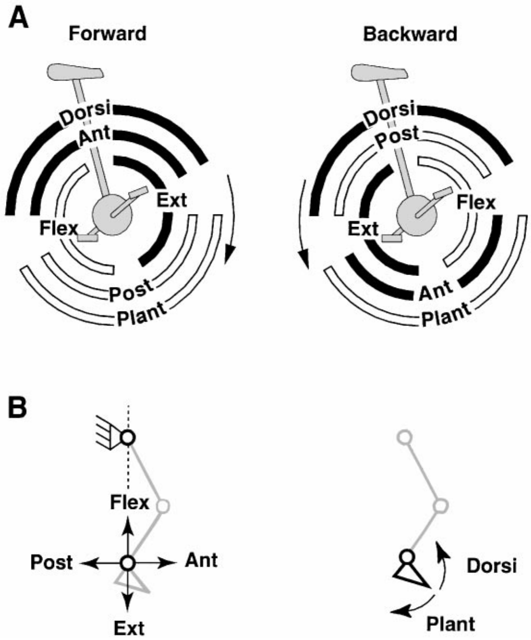

Fig. 1. Biomechanical functions from Ting et al. (1999) (used with permission): (A) the relative phasing of the six biomechanical functions organized into three pairs of alternating antagonistic functions. Backward pedaling is performed with a 180° phase shift of the Ant/Post pair; (B) the Ext/Flex pair accelerates the foot into extension/flexion with respect to the pelvis, the Ant/Post pair accelerates the foot anteriorly/posteriorly with respect to the pelvis, and the Plant/Dorsi pair accelerates the foot into plantarflexion/dorsiflexion.

Ting et al. (1999) inferred that a muscle performed the same function in each pedaling direction because the EMG timing was the same, but they did not present rigorous biomechanical analyses to assess whether a muscle performed the same biomechanical function, and if so, to what degree. While the EMG timing data appears to support a direction-dependent modulation of the muscles contributing to specific biomechanical functions, several questions remain unanswered. For example, the onset of rectus femoris activity occurred at the beginning of Ext near the top transition region (Bressel et al., 1998; Ting et al., 1999) when it appeared to be lengthening (i.e. the knee is flexing while the hip is extending). This result was somewhat unexpected, as previous studies have not suggested that muscles are active for significant regions of lengthening in pedaling (e.g. Hull and Hawkins, 1990; Neptune and Bogert, 1998). But it is possible that the rectus femoris still contributed to the Ext function through complex biomechanical mechanisms which are not apparent from analysis of experimental kinetic, kinematic and EMG data alone. For example, the paradoxical rectus femoris activity may have been necessary to transfer mechanical energy generated elsewhere (e.g. by another muscle) to propel the crank. A second question relates to why significant differences exist between the EMG magnitude of individual muscles in forward and backward pedaling (i.e. Bressel et al., 1998; Ting et al., 1999). Neither of these studies addressed whether the observed changes in the EMG magnitude in backward pedaling were necessary to adapt to changing task mechanics (e.g. are there direction-dependent changes in how a muscle contributes to a particular biomechanical function). If the EMG magnitude changes are not required to perform a biomechanical function similarly, then the neural control strategy is not completely determined by task mechanics.

Forward dynamic simulations are necessary to identify the contributions of individual muscles to the execution of specific biomechanical functions. Forward dynamic simulations allow the determination of a muscle's contribution to specific biomechanical functions and how these contributions change across different motor tasks (e.g.

Raasch and Zajac, 1999). Without forward dynamic analyses, it is difficult to identify the dynamic coupling between segments, muscle-induced accelerations and the biomechanical synergies associated with energy generation, absorption and transfer by individual muscles necessary to accelerate the crank.

Therefore, the objective of the present study was to use a forward dynamic simulation approach to theoretically examine previous experimental data in order to determine how muscles contribute to specific biomechanical functions during forward and backward pedaling. Specifically, we determined whether the observed changes in EMG magnitude were in response to different task mechanics, or whether the changes were a consequence of the pedaling neural control strategy being influenced by a factor independent of the task mechanics.

2. Methods

2.1. Simulation model

A planar two-legged bicycle-rider musculoskeletal model was generated using SIMM (MusculoGraphics, Inc., Evanston, IL). This simulation model was previously described in detail and will be reviewed briefly here (Neptune and Hull, 1998). The dynamical equations-of-motion for the model were derived using SD/FAST (Symbolic Dynamics, Inc., Mountain View, CA) and a forward dynamic simulation was produced by Dynamics Pipeline (MusculoGraphics, Inc., Evanston, IL). The model was driven by 14 individual Hill-type musculotendon actuators that were combined into nine muscles groups, with muscles within each group receiving the same excitation signal. The muscle groups were defined as PSOAS (iliacus, psoas), GMAX (gluteus maximus, adductor magnus), VAS (3-component vastus), HAMS (medial hamstrings, biceps femoris long), SOL (soleus), BFsh (biceps femoris short), GAS (gastrocnemius), RF (rectus femoris) and TA (tibialis anterior).

The individual muscle excitation patterns were modeled as block patterns defined by excitation onset, offset and magnitude and the activation dynamics were modeled by a first-order differential equation (Raasch et al., 1997). The excitation patterns between the left and right legs were considered symmetric and 180° out-of-phase. The effective crankload dynamics was modeled by an equivalent inertial and resistive torque applied about the center of the crankarm (Fregly, 1993).

Forward and backward pedaling simulations were produced using an optimization framework to identify the muscle stimulation patterns that reproduce the essential features of subject kinetic, kinematic and EMG data. The optimization algorithm was formulated to solve a tracking problem by finding the muscle stimulation patterns (muscle stimulation onset, offset and magnitude) that minimized the performance criterion:

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

where Y_{ij} are the experimentally measured data, $\hat{Y}_{ij}$ are the corresponding simulation data, SD_{ij} are the inter-subject standard deviations, n is number of data points and m is number of variables evaluated. The tracking quantities Y_{ij} included the radial and tangential pedal force components and pedal angle. The tracking problem was solved by converting the optimal control formulation into a parameter optimization (Pandy et al., 1992) and using a global optimization simulated annealing algorithm (Goffe et al., 1994). Simulations were performed over four revolutions to assure that initial start-up transients had decayed. The performance criterion (Eq. (1)) was evaluated during the fourth revolution when the simulation had reached its steady state, when it was considered to be independent of the initial conditions. A final time constraint was enforced to assure the simulations pedaled at the average experimentally measured pedaling rate ± 2 rpm.

From the pedaling simulation data, a power analysis was performed to quantify the muscular and non-muscular (gravity and velocity dependent forces) contributions to segment powers and accelerations (Fregly and Zajac, 1996). A segment power analysis was performed since it allowed the identification of individual muscle contributions to specific biomechanical functions and the synergistic mechanisms used to satisfy the task mechanics. Similar to Fregly and Zajac (1996) the segments were grouped together as limbs (ipsilateral foot, shank and thigh) and crank (the flywheel, freewheel, chainwheel, crank arms and pedals). An individual muscle may either generate (absorb) mechanical power to (from) the limbs, the crank or both, or transfer energy between the crank and limbs in either direction. These functions may also occur simultaneously (e.g. a muscle may transfer mechanical power between the limbs and crank while also generating energy to the crank or limbs). A muscle can contribute to the power of a segment (i.e. accelerate a segment) it does not touch through the intersegmental reaction forces (e.g. Fregly and Zajac, 1996). The net mechanical energy produced by a muscle over the crank cycle was computed by integrating the instantaneous muscle power (i.e. the product of the musculotendon force and velocity) over the crank cycle.

The linear transformation between segment power and acceleration (Fregly and Zajac, 1996) provides a clear interpretation of a muscle's influence on a segment: positive power generated by a muscle to a segment indicates that the muscle accelerated that segment. Accordingly, a muscle's contribution to specific biomechanical functions was determined by the muscle's ability to generate power to (or accelerate) the crank during the associated regions in the crank cycle (Fig. 1). For example, a muscle generating positive power through the extension region was considered as contributing to the Ext function, whether that power was delivered to the crank directly, or delivered to the segments where it could be transferred to the crank through synergistic muscles. Furthermore, a muscle that transfers positive power to the crank through the extension region contributes to the Ext function, even if its net power is negative.

2.2. Experimental data

To provide data for the tracking problem, the group average radial and tangential pedal force, and pedal angle trajectories from Ting et al. (1999) were used. Data were collected during forward and backward pedaling from 16 healthy subjects (eight male, eight female) at 60 rpm with a frictional workload of 120 (J cycle^{-1}). Further details about the data collection and processing can be found in Ting et al. (1999). All variables were referenced to a coordinate system attached to the seat post. The crank angle was defined 0° when the crank arm was parallel to the seat post with the leg in the most flexed position. Crank angle was positive in the direction of pedaling. Therefore, the limb extension phase corresponded to crank angles between 0 and 180° and the limb flexion phase corresponded to crank angles between 180 and 0° (Fig. 1).

3. Results

The kinetic, kinematic and muscle excitation data of the pedaling simulation closely matched the group averaged experimental data. The simulated pedal forces and pedal angle in both pedaling directions were almost

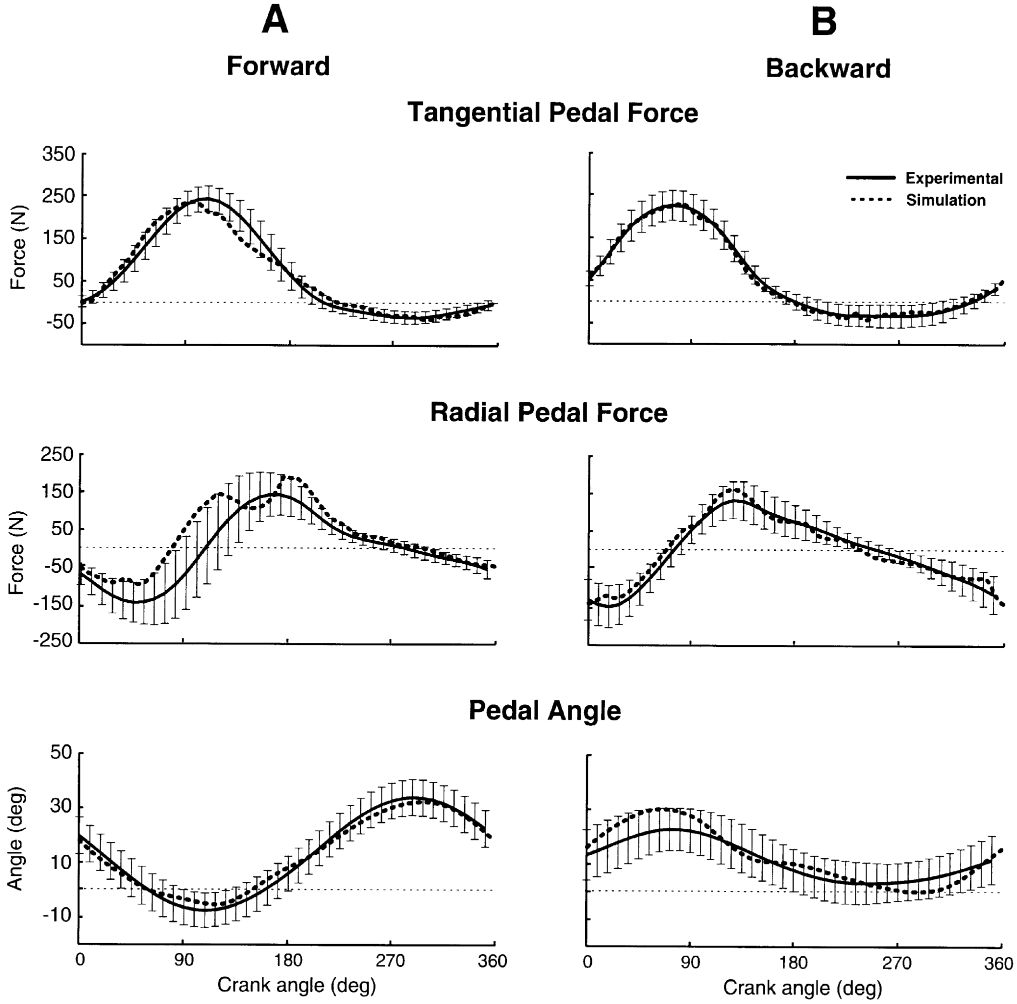

Fig. 2. Comparison of the simulation and group average experimental pedal force and pedal angle data of the right leg. The crank angle is 0° when the crank arm is parallel with the seat tube and the limb is in its most flexed position. The crank angle is positive in the direction of pedaling. Positive radial force is directed towards the crank center and positive tangential pedal force accelerates the crank. The pedal angle is relative to horizontal and positive when the foot is plantarflexed.

always within ± 1 SD of the experimental data (Fig. 2) and there was also close agreement between the muscle excitation and group EMG data (Figs. 4 and 5). The average simulation pedaling rates were 62 and 60 rpm for the forward and backward directions, respectively.

3.1. Backward pedaling

GMAX and VAS were active during the extension phase and produced 47% of the total mechanical energy generated by the muscles (Fig. 3). GMAX could not directly contribute to the pedal reaction force during the extension phase, therefore nearly all the energy generated by GMAX went to the limb segments that was transferred to the crank via other muscles and non-muscular forces (Figs. 4 and 6B). Energy generated by VAS went almost exclusively to directly accelerating the crank (Fig. 4). Both GMAX and VAS contributed to the Ext function since they either directly or indirectly accelerated the crank by working synergistically with other muscles (see below) during the extension region.

Both SOL and GAS contributed to the Plant function during the extension phase and transferred energy from the limbs to the crank. SOL was co-excited with VAS and GMAX (early extension phase) and functioned synergistically to transfer much of the limb segment energy being generated by VAS and GMAX to the crank. GAS was excited for the later portion of the extension phase (after SOL), effectively transferring additional mechanical energy stored in the limbs to the crank (Figs. 4 and 6B). While the primary functions of SOL and GAS were to transfer energy generated elsewhere, both muscles also generated small amounts of energy directly to the crank (net power during active regions is positive). Then during the upstroke, both SOL and GAS transferred energy from the crank to the limbs (restoring its kinetic and potential energy) by preventing the ankle joint from collapsing.

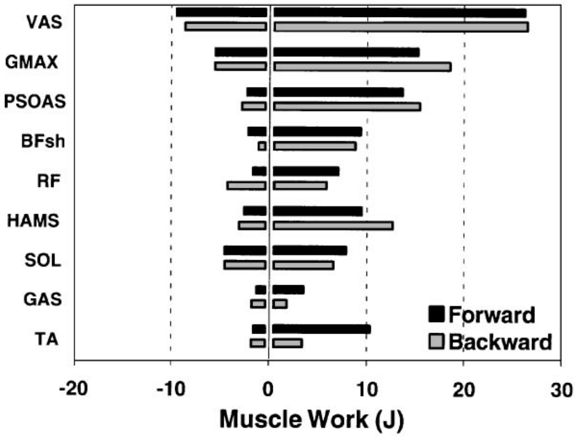

Fig. 3. Right-leg positive and negative muscle work produced over the crank cycle in both pedaling directions. Positive values indicate muscle work generated, negative values indicate muscle work absorbed.

Muscles contributing to the Flex function consisted of BFsh and PSOAS. BFsh and PSOAS together produced 31% of the total mechanical energy generated by the muscles (Fig. 3). Although both muscles functioned as agonists to accelerate the crank through the flexion phase, each used a different mechanism to accomplish the task. BFsh generated power directly to the crank while PSOAS worked synergistically with TA by generating energy to the limb segments while TA transferred the energy to the crank (Fig. 4). HAMS contributed to the Post function by directly accelerating the crank posteriorly through the top transition region (Fig. 4). RF contributed to the Ext and Ant functions with an eccentric work phase (early extensor phase) followed by a concentric work phase (through the bottom transition region). During the eccentric work phase, RF absorbed energy from the limb segments and transferred some of the energy it absorbed to the crank, while during the concentric work phase, RF directly accelerated the crank.

3.2. Forward pedaling

The muscles performing the Ext/Flex and Plant/Dorsi functions were similar to backward pedaling. VAS and GMAX produced 37% of the total mechanical energy generated by the muscles (Fig. 3). The energy generated by GMAX went to the limb segments, while VAS generated energy to both the limb and crank segments (Fig. 5). At the beginning of the extension phase, VAS generated energy directly to the crank since it could contribute to the pedal reaction force (Fig. 5). Then, VAS distributed similar amounts of energy to both the crank and limbs during the second half of its excitation phase. As VAS deactivated during the upstroke, it absorbed energy from the crank. Similar to backward pedaling, GAS, SOL and TA worked synergistically to transfer energy from the limb segments to the crank. The phasic activity of PSOAS and BFsh and their functions were similar to backward pedaling and combined to produce 26% of the total mechanical energy generated by the muscles (Figs. 3 and 5).

Distinct differences from backward pedaling were observed in the muscles contributing to the Ant and Post functions as a result of the different limb kinematics and muscle excitation phasing. A timing shift of nearly 180° allowed HAMS to directly propel the crank posteriorly through the bottom transition region (Fig. 5). A timing shift in RF muscle activity allowed RF to contribute to the Ant and Ext functions by accelerating the crank anteriorly through the top transition region. RF accelerated the crank by generating positive energy to the limbs that was transferred by TA during the late flexion phase, and then by transferring energy from the limbs to the crank during the early extension phase.

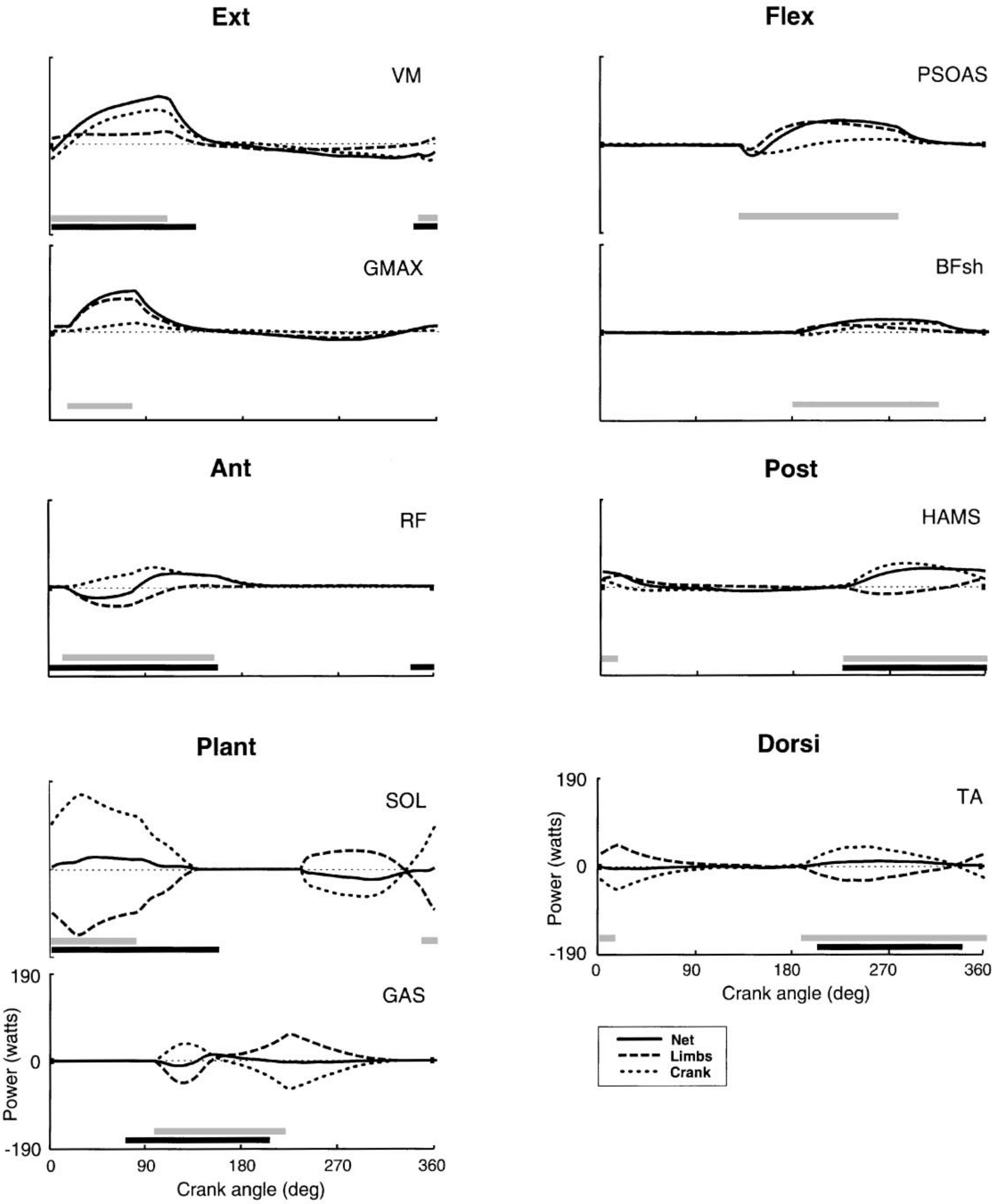

Fig. 4. Right-leg mechanical power produced by each muscle during the crank cycle in backward pedaling. The net power is the sum of the power generated to the limb and crank segments. Positive (negative) power indicates energy generation (absorption). The black horizontal bars correspond to the simulation excitation timing for that muscle while the gray horizontal bars correspond to the group average EMG timing estimated from Ting et al. (1999).

4. Discussion

To successfully complete the pedaling task, a cyclist must accelerate the crank against a frictional and inertial load. The simulation data and mechanical energy analysis allowed us to investigate the energy contributions of individual muscles and non-muscular forces to the acceleration of the crank. A flow of positive power to the crank indicates crank acceleration, whereas a negative flow indicates crank deceleration. Further, the mechanical energy analysis allowed us to investigate the individual muscle contributions to specific biomechanical functions and how these contributions change during the different pedaling tasks. The non-muscular forces, being conservative, could only transfer energy between the limbs and crank (Fregly and Zajac, 1996) and did so similarly in both pedaling directions (Fig. 6). Although phase reversal of the Ant/Post functions were required to

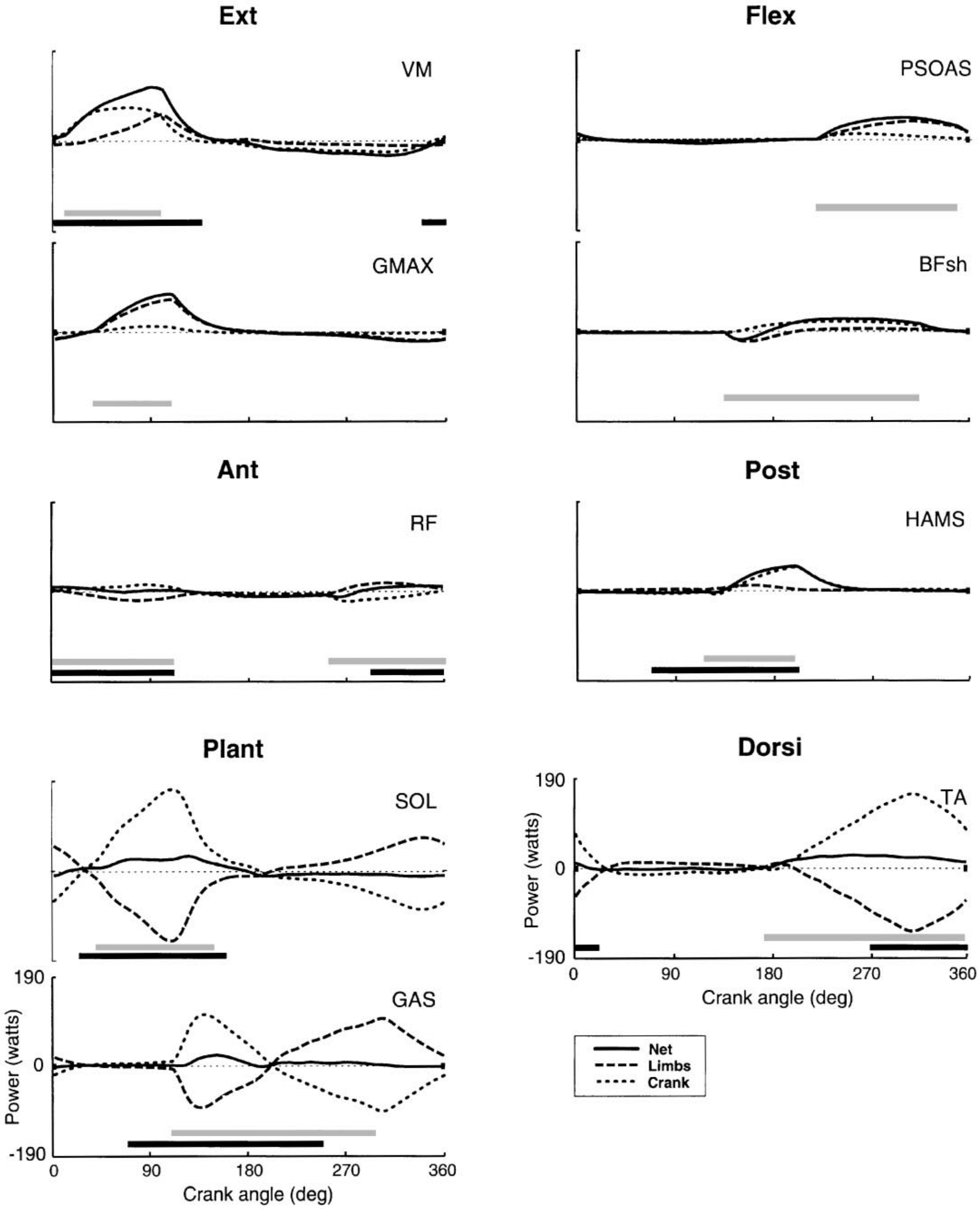

Fig. 5. Right-leg mechanical power produced by each muscle during the crank cycle in forward pedaling.

adapt to the changing task mechanics of forward and backward pedaling, individual muscle contributions to the specific biomechanical functions did not change between the two pedaling tasks.

The muscles contributing to the Ext biomechanical function (VAS and GMAX) produced the majority of the total energy delivered to the crank in both forward (37%) and backward (47%) pedaling, which was consistent with the analysis of maximum speed pedaling (Raasch et al., 1997). SOL was co-excited to work synergistically with VAS and GMAX in both pedaling directions to serve as the primary energy transfer mechanism by acting to stiffen the ankle joint. Since GMAX generates more energy to the limb segments than VAS, a coupling between GMAX and SOL EMG activity would be expected. During forward pedaling, Neptune et al. (1997) found that the GMAX and SOL iEMG varied in the same non-linear fashion across different pedaling rates while most other muscles varied linearly. The synergistic relationship between SOL and the Ext muscles was further supported in backward pedaling. There was a reduction in the energy VAS generated to the limb segments that

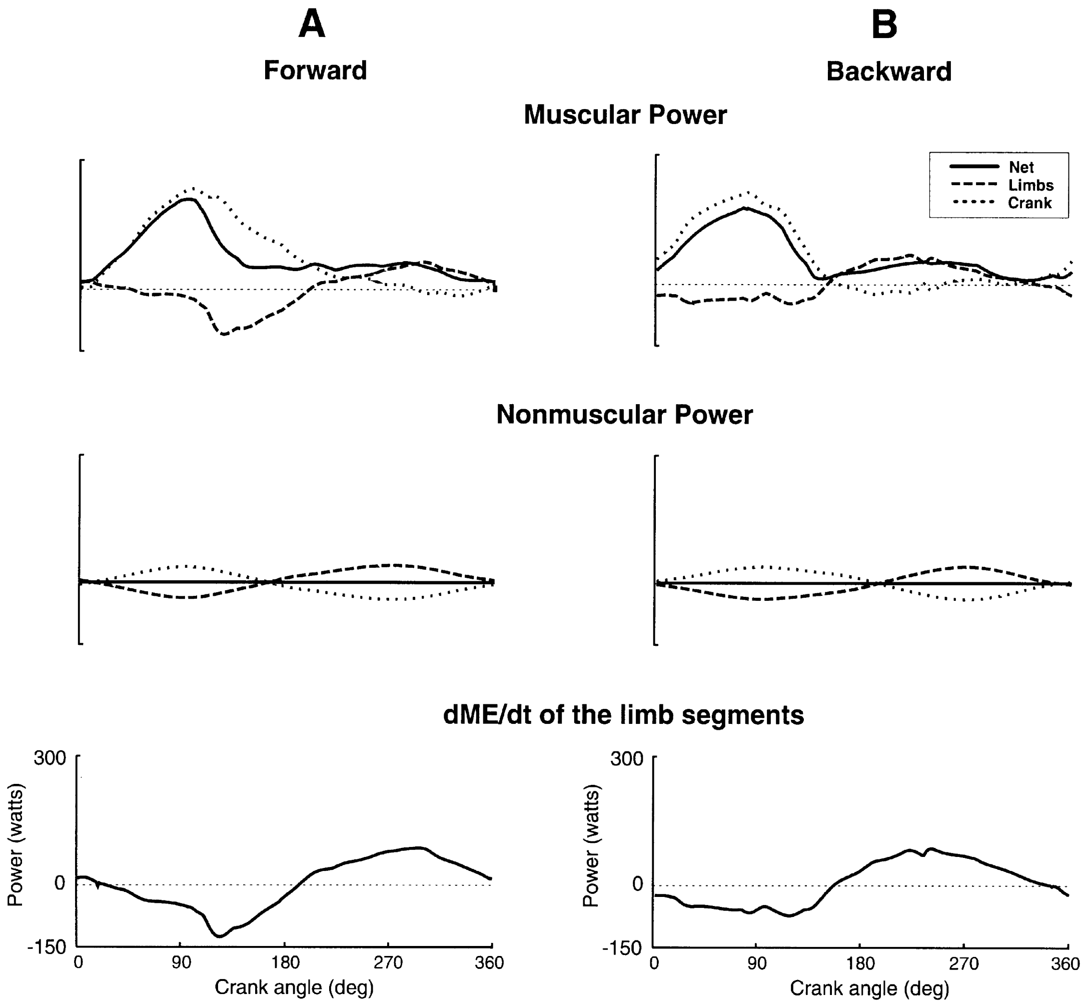

Fig. 6. Right-leg total mechanical power produced by all muscular and non-muscular forces (gravity and velocity-dependent forces) and the time rate of change of mechanical energy of the right limb segments during the crank cycle in (A) forward pedaling, and (B) backward pedaling.

corresponded with a significant decrease in the SOL iEMG and the total energy transferred by SOL (Ting et al., 1999; Figs. 4 and 5).

Both SOL and GAS contributed to the Plant function with different phasing independent of pedaling direction. SOL functioned synergistically with the Ext muscles to transfer power to the crank while GAS functioned late in the extension phase to transfer kinetic and potential energy stored in the limb segments to the crank (Figs. 4–6). This result supports previous studies suggesting that GAS is an important muscle in accelerating the crank through the bottom transition region (Neptune et al., 1997; Raasch et al., 1997). The correlation between GAS activity and the segment mechanical energy suggests that GAS would play a more important role as pedaling rate increases, which is supported by EMG data showing that GAS is highly pedaling rate sensitive (e.g. Neptune et al., 1997). During backward pedaling, there was a decrease in the amount of limb segment energy transferred to the crank during the bottom transition region (Fig. 6B). The correlation between the amount of limb segment energy transferred and GAS activity is supported by experimental data showing GAS iEMG significantly decreases during backward pedaling (Bressel et al., 1998; Ting et al., 1999).

Bressel et al. (1998) observed a significant increase in VAS activity in backward versus forward pedaling that may be the result of the neuromuscular system taking advantage of VAS's ability to directly accelerate the crank (Ting et al. 1999 also showed a slight trend towards an increase in VAS iEMG during backward pedaling, although the increase was not statistically significant). During forward pedaling, all of the energy generated by VAS did not directly accelerate the crank (Fig. 5). Instead, VAS also generated energy to the limb segments that was transferred to the crank through co-excitation of SOL. But during backward pedaling, VAS not only generated nearly all its energy directly to the crank, but was also able to be activated longer to accelerate the crank as it had the mechanical advantage of a longer region of muscle shortening (Fig. 4). These results suggest the neuromuscular system may be taking advantage of the increased ability of VAS to generate power directly to the crank, as opposed to power generated to the limb segments that requires synergistic SOL co-excitation in order for the crank to be accelerated. Note that Ting et al. (1999) found SOL iEMG was significantly reduced in backward pedaling which supports this mechanism.

Similar to the Plant and Ext synergistic pair, a second synergistic pair was observed between Flex and Dorsi during both forward and backward pedaling. PSOAS generated energy to the limb segments during the flexion phase while TA transferred the energy to the crank by stiffening the ankle joint. The region of muscle shortening was nearly identical for PSOAS in both pedaling directions, and therefore, no changes were observed in the phasing of PSOAS activity in the simulation data (Figs. 4 and 5). Fregly and Zajac (1996) did not observe an ankle–hip flexor synergy in their power analysis of pedaling at the joint torque level. The ankle's net extensor joint torque throughout the flexion phase masked the co-contraction between TA and GAS and the important ankle–hip flexor synergy between PSOAS and TA. BFsh also functioned similarly during both pedaling tasks, although the region of muscle shortening shifted later in the crank cycle in backward pedaling.

Thus, the muscles contributing to the Ext/Flex (VAS, GMAX, PSOAS, BFsh) and Plant/Dorsi (SOL, GAS, TA) functions were insensitive to pedaling direction and their functional roles were consistent with other experimental and theoretical studies (Neptune et al., 1997; Raasch et al., 1997; Ting et al., 1999; Raasch and Zajac, 1999). But, substantial differences in phasing were observed in muscles contributing to the Ant/Post (RF, HAMS) functions as predicted by the change in task mechanics and consistent with experimental data (Bressel et al. 1998; Ting et al. 1999).

The primary role of the muscles contributing to the Ant/Post functions is to accelerate the crank through the transition regions to prevent the flywheel from decoupling from the crank (Neptune et al., 1997; Raasch et al., 1997). Factors contributing to the crank deceleration in this region include both the low bilateral energy transfer to the crank and the loss of stored mechanical energy in the limb segments (Fig. 6). Hence, HAMS and RF activity is necessary to provide a smooth transition between the extension/flexion and flexion/extension transitions, respectively.

During forward pedaling, HAMS directly accelerated the crank through the extension–flexion transition with peak power occurring just prior to 180°. This result was different than Raasch et al. (1997) who found HAMS generated energy to the limb segments during late extension phase and then to the crank through the bottom transition region. The difference between the two studies is most likely related to the difference in the pedaling task. Raasch et al. (1997) examined maximum speed pedaling that required maximum energy generation throughout the crank cycle. During the sub-maximal pedaling conditions of the present study, the duration of HAMS activity was decreased and only necessary to help accelerate the crank through the bottom transition region. During backward pedaling, HAMS activity was phase advanced nearly 180° and contributed to the Post function by accelerating the crank through the top transition region. Beyond the flexion–extension transition, HAMS generated energy to the limb segments that was transferred to the crank primarily by SOL.

Perhaps the most intriguing result of this study was the paradoxical RF activity that could be assessed through the simulation-based analysis. Experimental studies of backward pedaling have shown that cyclists activate RF shortly after the flexion–extension transition when the RF muscle is apparently lengthening (Bressel et al., 1998; Ting et al., 1999). The negative net energy absorbed by RF during the early extension phase indicates RF is indeed lengthening during this region, but a portion of this eccentric muscle work is used to transfer energy generated elsewhere (primarily VAS and GMAX) to accelerate the crank. The smaller shift (compare to HAMS) and early offset in RF EMG activity during backward pedaling led Ting et al. (1999) to suggest that RF contributes primarily to the Ext function, rather than to both Ext and Ant as in forward pedaling. However, our simulations of the same data showed that even though the RF excitation ceased before the extension–flexion transition, RF still contributed to the Ant function by accelerating the crank through the first half of the Ant region while the muscle was still shortening and deactivating (Fig. 4). Note that increasing VAS output in this region would have served the same purpose without producing significant negative work. But previous pedaling simulations of forward pedaling have shown that RF activity during the flexion/extension transition region is necessary to provide a smooth pedaling trajectory (Raasch and Zajac, 1999). Perhaps the co-excitation of VAS and RF are reflective of the neural control strategy learned for forward pedaling. Further study is needed to assess whether long-term motor learning will affect the neural control strategy used during backward pedaling.

The pedaling simulations proved necessary to interpret the experimental data and identify motor control mechanisms used to accomplish specific motor tasks, as the mechanisms are often complex and not always intuitively obvious. For example, the simulation data was necessary to understand RF behavior in backward pedaling. In addition, the simulation data allowed individual muscle lengths to be investigated, which were not considered in previous experimental examination of forward and backward pedaling. Regions of muscle shortening are not inverted in the crank cycle when switching from forward to backward pedaling. However, regions can be longer or shorter depending on the pedaling direction (e.g. VAS's longer shortening region in backward pedaling). These results illustrate utility of theoretical analyses combined with experimental data to increase our understanding of movement control.

The simulation results showed that muscles contributed to the same biomechanical functions in both pedaling directions and that changes in muscle excitation magnitude were largely dictated by a muscle's ability to contribute to specific functions. These results also suggest a simplified control strategy that generates muscle activation patterns based on a muscle's ability to contribute to specific biomechanical functions to achieve the desired motor task. Future investigations are needed to determine how much this control depends on afferent feedback modulation of a common pattern for pedaling, and how much it depends on the nervous system having an accurate internal model of how muscles contribute to each biomechanical function.

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