A STATE-SPACE ANALYSIS OF MECHANICAL ENERGY GENERATION, ABSORPTION, AND TRANSFER DURING PEDALING

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Abstract—Seated ergometer pedaling is a motor task ideal for studying basic mechanisms of human bipedal coordination because, in contrast to standing and walking, fewer degrees of freedom are being controlled and upright balance is not a factor. As a step toward understanding how individual muscles coordinate pedaling, we investigated how individual net muscle joint torques and non-muscular (e.g. centripetal, coriolis, and gravity) forces of the lower limbs generate, absorb, and transfer mechanical energy in order to propel the crank and recover the limb. This was accomplished using a mechanical power analysis derived entirely from the closed-form state-space dynamical equations of a two-legged pedaling model that accounted for both the limb segmental and crank load dynamics.

Based on a pedaling simulation that reproduced experimental kinematic and kinetic trajectories, we found that the net ankle and hip extensor joint torques function 'synergistically' to deliver energy to the crank during the downstroke. The net hip extensor joint torque generates energy to the limb, while the net ankle extensor joint torque transfers this energy from the limb to the crank. In contrast, net knee extensor and flexor joint torques function 'independently' by generating energy to the crank through the top and bottom of the stroke, respectively. The net ankle joint torque transfers and the net knee joint torque generates energy to the crank by contributing to the driving component of the pedal reaction force. During the upstroke, net ankle extensor joint torque transfers energy from the crank to the limb to restore the potential energy of the limb. In both halves of the crank cycle, gravity forces augment the crank–limb energy transfer performed by the net ankle extensor joint torque.

Keywords: Lower limb; Biomechanics; Coordination; Computer simulation.

INTRODUCTION

Stationary ergometer pedaling is a task requiring intra- and inter-limb coordination to propel the crank through a constrained path. This constraint reduces the mechanical degrees of freedom being controlled, making pedaling coordination more amenable to investigation than, say, walking coordination. Furthermore, when subjects are seated while pedaling, balance is not a factor in accomplishing the task, as in walking. One additional benefit is that the external frictional and inertial load of the ergometer can be manipulated to study the corresponding changes in muscular function (e.g. Ericson et al., 1986). Ergometer pedaling is, therefore, a motor task ideal for studying basic mechanisms of bipedal coordination.

Pedaling requires that the mechanical energy produced by the muscles be transferred to the crank to overcome the frictional and inertial load of the ergometer. As a first step toward understanding how muscles accomplish this, the mechanical power developed by each net muscle joint torque of the leg has been computed by multiplying each joint torque (i.e. as obtained from an inverse dynamics analysis) with the corresponding joint angular velocity (e.g. Ericson, 1988; Ericson et al., 1986). By computing the joint powers associated with different frictional loads, Ericson (1988) found that the net knee and hip extensor joint torques produce substantial mechanical energy to propel the crank. However, the biomechanical mechanism by which this mechanical energy flows through the limb segments to the crank was not elucidated.

For this reason, a free-body power analysis of the entire limb has been used to analyze mechanical energy flow during pedaling (Ingen Schenau et al., 1990). This approach utilizes a free-body power equation (e.g. Robertson and Winter, 1980) which computes the energy flow through a generic segment due to the net muscle joint torques and the intersegmental reaction forces acting on the segment. By summing the power equations for the foot, shank, and thigh segments, a single power equation for the entire limb is obtained which contains no intersegmental reaction forces except those acting at the two ends of the kinematic chain (Aleshinsky, 1986; Ingen Schenau and Cavanagh, 1990). In the case of pedaling, this equation shows how the summed power produced by the net muscle joint torques is decomposed into the power (i.e. rate of change of energy) contributed to the crank through the pedal reaction force and the rate of change of mechanical energy of the limb (Ingen Schenau et al., 1990). Even so, because a free-body power analysis cannot fully decompose the power contributed to the crank and limb, it does not reveal how net muscle joint

Received in final form 15 November 1994.
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torques act in synergy among themselves and with non-muscular (e.g. centripetal, coriolis, and gravity) forces to deliver energy to the crank.

A state-space power analysis permits the full decomposition of crank and limb mechanical power into muscular (e.g. net muscle joint torques) and non-muscular (i.e. centripetal, coriolis, gravity, and friction) components. This is because a state-space approach accounts for how each force and torque influences the dynamics of each modeled segment, even those to which it is not applied directly (e.g. the crank; Fregly and Zajac, 1989). To implement this approach, closed-form state-space dynamical equations, such as those used to study and design multi-input multi-output control systems (Franklin et al., 1986), must be derived for the specific task under investigation. These equations have been used previously to define how each muscle force acts to accelerate each modeled segment (Hatze, 1987; Zajac and Gordon, 1989). Such knowledge can be pivotal for understanding CNS control strategies (Kuo and Zajac, 1993a), muscle coordination of multi-joint motor tasks (Hatze, 1976, 1980; Pandy and Zajac, 1991; Zajac, 1993, Zajac and Levine, 1979), and how muscle strength may limit movement (Kuo and Zajac, 1993b).

This paper uses a state-space power analysis to determine how net muscle joint torques and non-muscular forces cause mechanical energy to flow into or out of each modeled segment, including the crank. Analysis of how mechanical energy is generated, absorbed, and transferred reveals whether net muscle joint torques function 'synergistically' or 'independently' to propel the crank, which is an important step toward understanding the coordination of individual muscles during pedaling.

THEORY AND METHODOLOGY

Dynamical pedaling model

We developed a three degree-of-freedom, two-legged dynamical model of stationary ergometry pedaling (Fig. 1), consistent with Ingén Schenau and Cavanagh's (1990) recommendation that the entire system of athlete and equipment be considered in biomechanical power analyses. Each leg was considered to be part of a planar five-bar linkage, where the crank angle \( \theta_1 \) and the two foot segment angles \( \theta_2 \) and \( \theta_3 \) with respect to an inertial reference frame were selected to be the three generalized coordinates. Although only one leg needs to be modeled to calculate net muscle joint torques via an inverse dynamics approach, both legs and their interaction with the crank (i.e. the crank load dynamics) must be modeled in order to decompose the mechanical power of the crank. The crank load dynamics were modeled using an 'effective' frictional and inertial load (Fregly, 1993).

The computer program Autolev (Levinson and Kane, 1990; Schaechter and Levinson, 1988) based on Kane's method (Kane and Levinson, 1985) was used to derive the closed-form state-space dynamical equations. Due to their excessive length and complexity, only their form will be presented here. The Autolev input file used to derive the equations and the energy conservation method used for checking the equations are, however, available (Fregly, 1993).

Contributions to the angular acceleration of the crank and limb segments

The closed-form state-space dynamical equations for the above model define how each net muscle joint torque and non-muscular force contributes to the angular acceleration of the crank and limb segments (Fregly and Zajac, 1989). Briefly, if each generalized speed is defined as the first time derivative of the corresponding generalized coordinate, then the three degree-of-freedom dynamical equations can be expressed in matrix form as

\[
\begin{align*}
\mathbf{M}\ddot{\mathbf{\theta}} &= \mathbf{T}(\mathbf{\theta}) + \mathbf{V}(\mathbf{\theta}, \dot{\mathbf{\theta}}) + \mathbf{G}(\mathbf{\theta}) + \mathbf{F},
\end{align*}
\]  

where

\[
\begin{align*}
\mathbf{0} &= [\theta_1, \theta_2, \theta_3]^T \\
\mathbf{M}(\mathbf{\theta}) &= 3 \times 3 \text{ mass matrix, which depends on the configuration and inertial properties of the crank and body segmental linkage} \\
\mathbf{T}(\mathbf{\theta}) &= 3 \times 1 \text{ column matrix due to net muscle joint torques} \\
\mathbf{V}(\mathbf{\theta}, \dot{\mathbf{\theta}}) &= 3 \times 1 \text{ column matrix due to angular velocity of the segments (i.e. centripetal and coriolis forces)} \\
\mathbf{G}(\mathbf{\theta}) &= 3 \times 1 \text{ column matrix due to gravity forces} \\
\mathbf{F} &= 3 \times 1 \text{ column matrix due to frictional forces.}
\end{align*}
\]

Because F in this model is calculated from the average power over one cycle, as determined from experimental pedal force measurements, it accounts for not only flywheel belt friction but also chain friction, bearing friction, flywheel wind friction, and any other frictional effects experienced by the cyclist at the crank. If hip motion were
modeled, we could add four degrees-of-freedom (i.e. two translations for each hip joint) and two forces (i.e. one reaction force vector for each hip joint) to the model to account for the upper body and trunk dynamics. The resulting seven degree-of-freedom dynamical equations would have the same form as equation (1) except for an additional column matrix on the right-hand side due to the hip joint reaction forces.

Because $M(\theta)$ is non-singular for realistic limb trajectories (e.g. no knee hyperextension), both sides of equation (1) can be premultiplied by $M^{-1}(\theta)$ to determine how each muscle, velocity-dependent, gravity, and friction force and/or torque contributes to the total angular acceleration of the crank and the two foot segments:

$$\ddot{\theta} = M^{-1}(\theta)T(\theta) + M^{-1}(\theta)V(\theta, \dot{\theta}) + M^{-1}(\theta)G(\theta) + M^{-1}(\theta)F.$$  \hspace{1cm} (2)

Since the shank and thigh kinematics depend on the crank and foot kinematics (i.e. as found by differentiation of the five-bar linkage configuration constraint equations), the total angular acceleration of the two shank and two thigh segments can also be decomposed into contributions from muscle, velocity-dependent, gravity, and friction terms. Thus, given a cycling trajectory $\theta(t)$ and $\dot{\theta}(t)$ and the net muscle joint torques which produce it, we can compute how any torque or force in the model contributes to the angular acceleration of any modeled segment (e.g. the crank).

$M^{-1}(\theta)$ defines, therefore, the instantaneous linear relationship between each net muscle joint torque and the angular acceleration of each segment. Because $M^{-1}(\theta)$ is non-diagonal, a net muscle joint torque generally contributes to the angular acceleration of all segments, even those on which it does not act directly (often referred to as ‘dynamic coupling’; Zajac and Gordon, 1989). Pedaling illustrates this fact well since muscle joint torques are not applied directly to the crank, yet they are essential for accelerating the crank (i.e. via their contribution to the pedal reaction forces).

**Contributions to the mechanical power of the crank and limb segments**

A state–space approach can also be used to define how each muscular and non-muscular component contributes to the mechanical power of the crank and the body segments. Consider a dynamical system described by equation (1), where each generalized speed is defined as the first time derivative of the corresponding generalized coordinate (the most common case) and where no prescribed motions as a function of time are considered to occur. Then regardless of whether the system is holonomic (i.e. no motion constraints) or non-holonomic (i.e. motion constraints, the case here), the expressions appearing in equation (1) are related to KE, the system kinetic energy, by (Kane and Levinson, 1985)

$$dKE \frac{dt}{dt} = [M(\theta)\ddot{\theta} - V(\theta, \dot{\theta})]^T \dot{\theta}$$  \hspace{1cm} (3)

and to PE, a system potential energy, by (Kane and Levinson, 1985)

$$dPE \frac{dt}{dt} = -G(\theta)^T \dot{\theta},$$  \hspace{1cm} (4)

where $-M(\theta)\ddot{\theta} + V(\theta, \dot{\theta})$ are the generalized inertia forces, $G(\theta)$ are the generalized active forces assuming no applied forces and torques other than gravity, $\dot{\theta}$ are the generalized speeds, and the superscript T indicates matrix transposition. Based on equations (3) and (4), the mechanical power $P$ of the entire system, defined as the first time derivative of its total mechanical energy $E = KE + PE$, is:

$$P = [M(\theta)\ddot{\theta} - V(\theta, \dot{\theta}) - G(\theta)]^T \dot{\theta}.$$  \hspace{1cm} (5)

Furthermore, the mechanical power $P_i$ of any individual segment $i$ can be found from equation (5) by setting all masses and inertias to zero except the mass and inertia of segment $i$:

$$P_i = [M_i(\theta)\ddot{\theta} - V_i(\theta, \dot{\theta}) - G_i(\theta)]^T \dot{\theta},$$  \hspace{1cm} (6)

where the subscript $i$ on the right-hand side of equation (6) indicates that only the mass and/or inertia of segment $i$ appear in these matrices. A positive (negative) value of $P_i$ means that mechanical energy is flowing into (out of) the segment.

The fact that $\ddot{\theta}$ appears linearly in equation (6) and can be decomposed into muscular and non-muscular components via equation (2) means that the total mechanical power $P_i$ of any modeled segment $i$ can be partitioned into contributions from each muscle, velocity-dependent, gravity, and friction force and/or torque:

$$P_i = \left[\begin{array}{l} \frac{\ddot{\theta}^{\text{Muscle}}}{P_i^{\text{Muscle}}} \\
\frac{\ddot{\theta}^{\text{Velocity}}}{P_i^{\text{Velocity}}} \\
\frac{\ddot{\theta}^{\text{Gravity}}}{P_i^{\text{Gravity}}} \\
\frac{\ddot{\theta}^{\text{Friction}}}{P_i^{\text{Friction}}} \end{array}\right].$$  \hspace{1cm} (7)

Thus, given a cycling trajectory $\theta(t)$ and $\dot{\theta}(t)$ and the net muscle joint torques which produce it, equation (7) defines the explicit mathematical relationship between any torque or force in the model and the mechanical power it contributes (positive or negative) to any modeled segment, including the crank. Since the total mechanical power of a segment can be expressed in terms of the net joint torques and the intersegmental forces acting on this segment (consider a free-body diagram), the state–space approach (i.e. equation (7)) implicitly accounts for the intersegmental reaction forces by decomposing them (see Discussion).

Because power is a scalar quantity, individual segment powers can be summed to determine the power a net muscle joint torque contributes to any group of segments.
(Fregly and Zajac, 1989), such as: (i) the crank (i.e. the flywheel, freewheel, chainwheel, crank arms, and pedals); (ii) the limb segments (i.e. the foot, shank, and thigh segments of both legs); and (iii) all the segments (i.e. the crank and limb segments together, yielding the net positive or negative power produced by the joint torque). Thus, if there are n segments in the model, with segments 1 through m associated with the crank and segments m + 1 through n associated with the limbs, then

$$\sum_{i=1}^{n} P_i = \sum_{i=1}^{m} P_i + \sum_{i=m+1}^{n} P_i$$

(8)

where each $P_i$ is computed from equation (7) by assuming all forces and torques are zero except the net muscle joint torque whose mechanical power contribution is to be computed. Equation (8) therefore defines how the net power (i.e. $P_{Net}$) provided by a net muscle joint torque is distributed between the crank (i.e. $P_{Crank}$) and the limb segments (i.e. $P_{Limbs}$), where $P_{Net}$ is equivalent to the product of the net muscle joint torque and the corresponding joint angular velocity. The power distribution due to any non-muscular torque or force (e.g. gravity) can be computed similarly.

**Mechanical energy generation, absorption, and transfer**

A net muscle joint torque may, theoretically, influence the mechanical energy of the crank and the limb segments in one of twelve ways (equation (8); Table 1). These 12 cases are combinations of three primary energy influences which a net muscle joint torque can exert on a dynamic system (Aleshinsky, 1986; Robertson and Winter, 1980). A net muscle joint torque may generate mechanical energy ($P_{Net} > 0$, cases 1–5 in Table 1) to either the crank, the limb segments, or both. In this situation, it functions as an energy source since it puts mechanical energy into the system. At other times, a net muscle joint torque may absorb mechanical energy ($P_{Net} < 0$, cases 6–10) from either the crank, the limb segments, or both. Here it acts as an energy sink since it takes mechanical energy out of the system. Finally, a net muscle joint torque may transfer mechanical energy ($P_{Crank}$ and $P_{Limbs}$ have opposite signs) from the limb segments to the crank or vice versa, while either simultaneously generating energy (cases 4 and 5), simultaneously absorbing energy (cases 9 and 10), or neither (cases 11 and 12). It then functions as an energy channel since it redistributes mechanical energy between the crank and the limb segments. It should be noted that a net muscle joint torque generates, absorbs, or transfers energy to or from

<table>
<thead>
<tr>
<th>Case</th>
<th>Net</th>
<th>Crank</th>
<th>Limbs</th>
<th>Power plot features</th>
<th>Primary energy influences</th>
<th>Generated to/(absorbed from)</th>
<th>Transferred from</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Net &gt; Crank</td>
<td>Generation</td>
<td>Crank and Limbs</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>Net = Crank</td>
<td>Generation</td>
<td>Crank</td>
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</tr>
<tr>
<td>3</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>Net = Limbs</td>
<td>Generation</td>
<td>Limbs</td>
<td></td>
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<tr>
<td>4</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>Crank &gt; Net</td>
<td>Generation and transfer</td>
<td>Crank</td>
<td>Limbs to Crank</td>
</tr>
<tr>
<td>5</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>Limbs &gt; Net</td>
<td>Generation and transfer</td>
<td>Limbs</td>
<td>Crank to Limbs</td>
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<td>6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Crank &gt; Net</td>
<td>Absorption</td>
<td>(Crank and Limbs)</td>
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<tr>
<td>7</td>
<td>–</td>
<td>–</td>
<td>0</td>
<td>Net = Crank</td>
<td>Absorption</td>
<td>(Crank)</td>
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<tr>
<td>8</td>
<td>–</td>
<td>0</td>
<td>–</td>
<td>Net = Limbs</td>
<td>Absorption</td>
<td>(Limbs)</td>
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<tr>
<td>9</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>Limbs &gt; Net</td>
<td>Absorption and transfer</td>
<td>(Crank)</td>
<td>Crank to Limbs</td>
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<tr>
<td>10</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>Crank &gt; Net</td>
<td>Absorption and transfer</td>
<td>(Limbs)</td>
<td>Limbs to Crank</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>+</td>
<td>–</td>
<td>Net = 0</td>
<td>Transfer</td>
<td>(Limbs)</td>
<td>Crank to Limbs</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>–</td>
<td>+</td>
<td>Net = 0</td>
<td>Transfer</td>
<td>(Crank)</td>
<td>Crank to Limbs</td>
</tr>
</tbody>
</table>
from the crank by contributing to the driving component of the pedal reaction force.

Similar analyses are helpful for understanding how non-muscular forces may influence mechanical energy flow. The effective friction force at the crank always absorbs mechanical energy ($P_{\text{net}} < 0$, cases 6–10) and always acts as an energy sink. Velocity-dependent and gravity forces, being conservative (Halliday and Resnick, 1981), can only transfer mechanical energy between the crank and the limb segments ($P_{\text{net}} = 0$, cases 11 and 12), again by their contribution to the driving component of the pedal reaction force. Thus, velocity-dependent and gravity forces can only act as energy channels (in this analysis, gravity is treated like any other force acting on the dynamical system). For a frictionless, revolute joint (e.g. the pedal, ankle, knee, and hip joints in our model), intersegmental reaction forces can only transfer energy between the two adjacent segments (Ingen Schenau and Cavanagh, 1990; Robertson and Winter, 1980). Because intersegmental reaction forces are a consequence of the forces/torques appearing in equation (1), the energy these intersegmental reaction forces transfer is accounted for automatically by a state-space power analysis.

Similar to the free-body power analysis used by Ingen Schenau et al. (1990) to study pedaling, the above state-space power analysis is only used to study the instantaneous flow of energy. Thus, no assumptions are made regarding mechanical energy expenditure as defined by Aleshinsky (1986) or the relative metabolic cost of positive versus negative net muscular power (e.g. see Williams, 1985).

Verification of dynamical pedaling model

Because a state-space power equation is model-dependent, we verified that our dynamical pedaling model (Fig. 1) can simulate experimental kinematic and kinetic trajectories. Nominal pedal reaction force, crank angle, and pedal angle trajectories were defined by averaging 10 consecutive cycles of right and left side data from 10 recreational male cyclists (age 27.5 ± 1.8 yr, height 1.80 ± 0.03 m, and weight 738 ± 67 N) (Fregly, 1993; Fregly et al., 1995). All subjects pedaled a Monark ergometer at 75 rpm with a 225 W workload, used cleated cycling shoes and toe clips, and exhibited similar pedaling kinematics and kinetics. Nominal net muscle joint torque trajectories were computed from the nominal force and angle trajectories using an inverse dynamics approach (Hull and Jorge, 1985; Redfield and Hull, 1986). Limb segment masses, mass centers, and moments of inertia were estimated from averaged subject weight and limb segment lengths using Dempster (1955). The resulting nominal experimental trajectories (Fig. 2) are similar to those reported elsewhere (Ericson et al., 1986; Hull and Jorge, 1985; Ingen Schenau et al., 1992, 1990; Redfield and Hull, 1986).

A dynamic simulation of two-legged pedaling was then computed using a parameter optimization algorithm (Pandy et al., 1992), where the cost function minimized the mean square error between experimental and simulated net muscle joint torque trajectories (i.e. optimal tracking). To produce a cyclic, symmetrical motion, we constrained the contralateral and ipsilateral net muscle joint torques to be equal and the final state (i.e. $\Theta$ and $\dot{\Theta}$ in equation (1)) to match the initial state. We quantified the resulting performance of the model by computing the root-mean-square (i.e. RMS) errors between the experimental and simulated trajectories. The crank angle, pedal angle, pedal force (brought into evidence via Kane's method), and net muscle joint torque trajectories were all tracked to within an acceptable 1% RMS error (maximum errors were small as well).

To check the mechanical power computations, we used the pedaling simulation found above to calculate the net power of the entire two-legged cyclist model using two approaches. First, an explicit expression for the total mechanical energy $E$ of the system was differentiated to calculate $dE/dt$. Second, equation (7) was used to compute the total power of each segment, and these segment powers were then summed to determine $P_{\text{net}}$ due to the simultaneous influence of all torques and forces in the
model. At each point in the crank cycle, we found that

\[ \frac{dE}{dt} = P_{\text{Net}}. \]  

\[ (9) \]

RESULTS

Using equations (7), (8), and Table 1, we investigated how net muscle joint torques, gravity forces, motion-dependent forces, and friction forces generate, absorb, and transfer energy between the crank and the limbs. Consider first the mechanical power distributions due to torques and forces acting on both limbs and the crank. Throughout the crank cycle, the six net muscle joint torques (i.e. three per limb) together primarily generate energy to the crank (Fig. 3(a), approximately case 2 in Table 1), while the effective frictional resistance torque primarily absorbs energy from the crank (Fig. 3(d), approximately case 7). In contrast, velocity-dependent and gravity forces transfer only small amounts of energy between the crank and the limb segments (Figs 3(b) and (c), cases 11 and 12). Thus the primary flow of mechanical energy during cycling is from the net muscle joint torques in the limbs to the frictional resistance at the crank (Ericson, 1988).

Consider next the mechanical power distributions due to torques and forces acting only on one limb. These torques and forces have virtually no mechanical power influence on the opposite limb (Table 1, caption). During the downstroke (0–180°), the three ipsilateral net muscle joint torques together generate energy to the crank while simultaneously transferring energy to the crank from the limb (Fig. 4(a), case 4). Ipsilateral gravity forces also transfer energy to the crank during most of the downstroke (Fig. 4(c), case 11). In the first half of the upstroke (180–270°), ipsilateral net muscle joint torques primarily generate energy to both the crank and the limb (Fig. 4(a), case 1), while in the second half (270–360°), they mainly generate energy to the limb while also transferring energy to the limb from the crank (case 5). Ipsilateral gravity forces augment this energy flow to the limb by transferring energy to the limb from the crank (Fig. 4(c), case 12). Over the entire crank cycle, ipsilateral velocity-dependent forces transfer only small amounts of energy (Fig. 4(b), cases 11 and 12). Thus, energy flows primarily to the crank in the downstroke and to the limb in the upstroke, and gravity forces as well as net muscle joint torques acting on the limb play an important role in this process.

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Fig. 3. Mechanical power distributions due to torques and forces acting on both limbs and the crank. (a) Bilateral net muscle joint torques, (b) bilateral velocity-dependent forces, (c) bilateral gravity forces, and (d) friction. Net is the power contributed to all segments in the model, including the crank, Crank is the power contributed to the crank segments, and Limbs is the power contributed to the segments of both limbs.

Thus, \[ \text{Net} = \text{Crank} + \text{Limbs}. \]
Finally, consider the mechanical power distributions due to individual net hip, knee, and ankle joint torques. The net hip joint torque primarily generates energy to the limb in the power stroke (Fig. 5(a), approximately case 3) and has very little mechanical energy influence in the recovery stroke. The net knee joint torque primarily generates energy to the crank over the entire crank cycle (Fig. 5(b), approximately case 2). The net ankle joint
torque primarily transfers energy, from the ipsilateral limb to the crank in the power stroke (Fig. 5(c), case 4 due to some energy generation to the crank as well), and from the crank to the limb in the recovery stroke (case 12).

DISCUSSION

The net hip and knee muscle joint torques produce most of the energy needed to propel the crank during pedaling (Ericson, 1988; Figs 5(a) and (b) solid lines). The state–space power approach shows how each net muscle joint torque, and each non-muscular force as well, contribute to the power of the crank and limb at each point in the crank cycle (Figs 3–5). This full decomposition of power is possible because the intersegmental reaction forces are implicitly being fully decomposed (i.e. the contribution of each torque and force to each intersegmental force is being accounted for and each contribution can be computed, if desired). A free-body power analysis is extremely limited in this regard. However, a state–space approach requires that a set of closed-form state–space dynamical equations describing the entire system consisting of subject and equipment be found. These equations are task-specific, can be difficult to derive, and are more difficult to validate (Zajac, 1993). In pedaling, the state–space approach requires not only a model of the body segments, as is required in the free-body approach, but also a dynamical model of the crank load (e.g. Fregly, 1993).

Net knee joint torque acts independently through top and bottom dead center

One way energy can be delivered to the crank is to have a net muscle joint torque act ‘independently’. The clearest example is where a net muscle joint torque, acting as an energy source, generates to the crank almost all of the energy it produces (Table 1, case 2). For this to happen, the net power produced by the net muscle joint torque must approximately equal the power it delivers to the crank through its contribution to the driving component of the pedal reaction force.

The net knee joint torque is the best example of a joint torque acting independently to deliver energy to the crank (Fig. 5(b); approximately case 2), most notably immediately after top dead center (TDC, 0°) and bottom dead center (BDC, 180°) of the stroke (Fig. 5(b), 0–90° and 180–270°). TDC and BDC are where crank torque produced by both legs is closest to zero, and thus where decoupling of the freewheel from the flywheel is most likely to occur (Fregly, 1993). Hence, net knee extensor joint torque at the beginning of the downstroke and net knee flexor joint torque at the beginning of the recovery stroke (Fig. 2(b), long dashed-line) are probably essential to prevent freewheel–flywheel decoupling.

Past work supports this notion that the net knee extensor and flexor joint torques act independently near TDC and BDC. Ericson (1988) found that the peaks in the net power curve from the knee joint torque increase near 45° and 225° when the frictional resistance of the ergometer is doubled. Hull and Jorge (1985) showed that when the frictional resistance is increased by about 20% during pedaling on rollers, the driving component of the pedal reaction force from 200° to 260° assists propulsion more, concomitant with a large increase only in the net knee flexor joint torque.

Net hip and ankle joint torques act synergistically during the downstroke

Another way energy can be delivered to the crank is to have two net muscle joint torques act in synergy. A highly restrictive example is where one net muscle joint torque acts only as an energy source, generating energy only to the limb segments (Table 1, case 3), and the other acts only as an energy channel, transferring the same energy to the crank (case 11). In this example, the joint torque acting as an energy source would not contribute to the driving component of the pedal reaction force. Otherwise it would also generate other energy to the crank (case 1) or also transfer other energy from the crank to the limb (case 5). The joint torque acting as an energy channel would, however, contribute to the driving component of the pedal reaction force in order to transfer the energy from the limb to the crank. On the other hand, the joint angular velocity would have to be zero; otherwise the net muscle joint torque would not be just an energy channel but would also be an energy source (generating energy, case 4) or an energy sink (absorbing energy, case 10).

The net ankle and hip joint torques seem to act in synergy during the downstroke. The net hip joint torque, being the energy source, produces much energy then (Fig. 5(a), solid line, 0–180°) and virtually all of it is generated to the ipsilateral limb (Fig. 5(a), short dashed line). The net ankle joint torque, being the energy channel, simultaneously transfers energy from the limb (Fig. 5(c), short dashed line) to the crank (Fig. 5(c), long dashed line) at about the same rate. Thus, the net ankle extensor joint torque (Fig. 2(b), solid line) acts in synergy with the net hip extensor joint torque (Fig. 2(b), short dashed line) during the downstroke because the net hip joint torque, by not being able to contribute to the driving component of the pedal reaction force, cannot alone deliver to the crank the energy it produces.

The existence of a net ankle and hip extensor joint torque synergy is supported by two important observations during the downstroke. First, relative to the net ankle joint torque, other energy channels transfer only a small amount of mechanical energy to the crank. This can be seen by analyzing how individual velocity-dependent and gravity forces (i.e. the only alternative energy channels) transfer mechanical energy between the crank and the ipsilateral limb in the downstroke. The mechanical power curves produced by any ipsilateral velocity-dependent or gravity force have the same shape as the mechanical power curves produced by all the ipsilateral velocity-dependent or gravity forces collectively (Figs 4(b) and (c)). Thus, the net ankle extensor joint torque is the only significant channel for transferring energy from the ipsilateral limb to the crank in the
downstroke (compare *Lims* curve in Fig. 5(c) with those in Figs 4(b) and (c)).

Second, relative to the net hip joint torque, other energy sources supply much less mechanical energy to the limb. One other energy source is the mechanical energy stored in the limb (primarily potential energy). We calculated that the limb loses 23 J of energy during the downstroke, leaving almost no stored mechanical energy at the bottom of the stroke. Another possible energy source is the hip joint reaction force (which in this situation would be treated like an applied force). Ingen Schenau et al. (1990) have estimated the energy flow through the hip joint during seated ergometer pedaling. Based on this power curve (their Fig. 5), we calculated that 12 J flowed through the hip joint into the thigh segment during the downstroke in their experiments. However, this is probably an upper limit in our experiments because a lower resistance torque should result in less hip motion (Neptune and Hull, 1995) and because a marker over the greater trochanter likely overestimates the movement of the true hip joint center (Neptune and Hull, 1995). Because the net hip joint torque in our subjects generates 38 J to the limb during the downstroke, the net hip joint torque is, therefore, a significant energy source to the limb (i.e. compare the 38 J from the net hip joint torque to the maximum of 35 J, minimum of 23 J, from the other sources).

Given the estimates above, it can be computed that between 50% and 82% of the energy generated to the limb by the net hip joint torque is transferred to the crank by the net ankle joint torque. During the downstroke, the net ankle joint torque always takes more energy out of the limb than the net hip joint torque puts in (compare Fig. 5(c), short dashed line, with Fig. 5(a), short dashed line). Thus, since the net ankle joint torque transfers 54 J from the limb to the crank (Fig. 5(c), short dashed line, 0–180°), it transfers as much as 82% of the energy generated to the limb by the net hip joint torque (assuming negligible hip motion, we have (54 – 23)/38 = 0.82, or 82%). Even if the maximum 12 J is transferred through the hip joint, the result is still 50% (i.e. (54 – 23 – 12)/38 = 0.5, or 50%).

We conclude that the net ankle and hip extensor joint torques act in synergy to deliver energy to the crank during the downstroke. Since Ericson (1988) found that a doubling of the ergometer frictional resistance causes the peaks in the net power curves of only the net ankle and hip joint torques to increase (near 120°), past work also supports this conclusion.

**Possible synergies during the upstroke**

A corollary to an ankle–hip extensor synergy in the downstroke is an ankle–hip flexor synergy in the upstroke, which is, mechanically, a theoretical possibility for delivering energy to the crank (Fregly, 1993). However, an ankle–hip flexor synergy is not used because an ankle extensor joint torque is produced throughout the upstroke (Fig. 2(b), solid line, 180–360°) and a hip extensor joint torque for half the upstroke as well (Fig. 2(b), short dashed line, 180–270°). In fact, the ankle extensor joint torque transfers energy from the crank to the limb in the upstroke (Fig. 5(c), 180–360°). Gravity forces in this region do the same (Fig. 4(c), 180–360°). Indeed, these two energy channels together restore the potential energy of the limb in the upstroke. A reason why an ankle–hip flexor synergy is not observed may be that energy delivery to the crank by the leg in the recovery stroke is inefficient because a substantial increase in net hip flexor joint torque would be necessitated and hip flexor muscles are weaker than hip extensor muscles (Hoy et al., 1990). Thus, it may be more efficient to let the downstroke leg produce the energy needed both for crank propulsion and for recovery of the upstroke leg rather than invoke an ankle–hip flexor synergy.

Finally, a knee flexor–ankle extensor synergy may exist to deliver energy to the limb in the upstroke (Figs 5(b) and (c): 180–315°). However, since gravity forces and net muscle joint torques of the contralateral downstroke leg deliver energy to the crank then (Figs 4(a) and (c), 0–135°), the energy transferred from the crank to the upstroke limb by the ankle extensor joint torque may not be the same energy generated to the crank by the net knee joint torque of the upstroke leg.

**Net muscle joint torque vs. muscle force coordination**

The state–space power analysis is equally applicable to the study of individual muscles and, if applied, may elucidate muscle synergies being used by the CNS to control pedaling. Clearly, the contribution of each muscle force to the mechanical power of the crank and each body segment can be found since the muscle joint torque(s) produced by each muscle is (are) given by its moment arm(s). The determination of the muscle forces, though difficult, is possible by ascribing dynamical properties to the muscles and including them in the state–space dynamical equations (e.g. Hatz, 1980; Zajac, 1989, 1993).

It is speculative to predict how individual muscles will coordinate energy flow to the crank based on a net joint torque analysis, as used here, because of the action of biarticular muscles (Ingen Schenau et al., 1992). Nevertheless, we conjecture that the uniaxial hip and ankle extensor muscles (e.g. gluteus maximus and soleus) will act in synergy during the downstroke and that the uniaxial extensor and flexor knee muscles will act independently at the limb flexion–extension transitions. A net joint torque study, such as this one, cannot hope to reveal the role of the biarticular muscles of the leg (e.g. hamstrings, rectus femoris, gastrocnemius).

**Acknowledgements**—We thank Gregory Woodward for his assistance with Autolev, Christine Dairaghi for her assistance with experimental data collection, Arthur Kuo for his insights regarding synergistic energy delivery, and Steven Kautz and Christine Raasch for their extensive comments on the manuscript. This paper is based on a Ph.D. dissertation (Fregly, 1993), which was supported by NIH grant NS17662, and the Rehabilitation R&D Service of the Department of Veterans Affairs.
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