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General Coordination Principles Elucidated by Forward Dynamics: Minimum Fatigue Does Not Explain Muscle Excitation in Dynamic Tasks

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The target article presents a framework for coordination of one- and two-joint muscles in a variety of tasks. Static optimization analyses were performed that minimize muscle fatigue, and it is claimed that the predicted muscle forces account for essential features of EMG activity "qualitatively" well. However, static optimization analyses use the observed joint moments, which implicitly assumes that they minimize the total muscle fatigue of the task. We use a forward dynamics (i.e., relationship between muscle forces and the kinematics and kinetics of task performance) modeling approach to show that this assumption does not appear to be true in cycling (which was used as an example task in the target article). Our results challenge the hypothesized coordination framework and the underlying concept that general coordination principles for dynamic tasks can be elucidated using inverse-dynamics-based analyses.

***Key Words*:** muscle coordination, forward dynamics simulation, inverse dynamics, pedaling

Consequences of Muscle Coordination: The Target Article View

The target article seeks to develop a framework for explaining the coordination of two-and one-joint muscles in a variety of tasks in order to "address the functional consequences of the observed muscle coordination." Muscle forces are predicted using inverse-dynamics-based static optimization (SO) analyses that minimize a muscle fatigue cost function. It is claimed that the predicted muscle forces account for essential features of EMG activity qualitatively well during a variety of tasks.

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Based on these results, the authors hypothesize that the functional consequences of the experimentally observed coordination patterns include reducing total muscle force, muscle fatigue, perceived effort, and mechanical and metabolic energy expenditure. Note that for dynamic tasks, such as walking, these measures are intended to apply globally to the entire movement, even though the optimizations were only done statically at each point in time. This means the authors are making the implicit assumption that the nervous system, presumably through evolution and learning, has found the muscle activation and joint moment patterns that minimize total muscle fatigue.

SO approach predicts muscles forces, not coordination. The SO approach has been used to predict muscle forces in many studies, as cited in the target article. However, often these studies (e.g., Crowninshield & Brand, 1981) were primarily interested in questions related to joint loading and orthopedic issues rather than the neural coordination of movement. We believe that explaining muscle coordination is much more complex than simply predicting force sharing between synergistic muscles. Even if the SO approach eventually proves to be a satisfactory predictor of muscle forces during dynamic tasks, it still cannot explain why a particular muscle produces force when it does. In contrast to static isometric tasks, in which a unique combination of joint moments exist for a given externally applied force, dynamic tasks can be accomplished using a near infinite combination of joint moments. For example, it has been shown that even though joint angle patterns are quite invariant during human walking, joint moments at the hip and knee are quite variable (Winter, 1983). In contrast to the target article's view of muscle coordination, we believe that understanding muscle coordination requires explaining *why* the nervous system produces a particular combination of joint moments for a given dynamic task. The target article does not explicitly address this fundamental question. Instead, it implicitly assumes that the experimentally observed joint moment patterns are consistent with the nervous system minimizing muscle fatigue.

Are the observed joint moments consistent with minimum fatigue? This is the crucial question. If the pattern of joint moments chosen by the nervous system to accomplish a task is not the pattern that minimizes the total muscle fatigue, then there is no basis for the theoretical framework for muscle coordination proposed in the target article. Static analyses such as those presented in the target article are not able to evaluate whether a particular pattern of joint moments minimizes the total muscle fatigue during a dynamic task. To do this one must investigate the range of possible joint moment patterns and calculate the total muscle fatigue for each one.

We have used a forward-dynamics-based approach to show that for at least one dynamic task, cycling, observed muscle coordination patterns do not appear to minimize total muscle fatigue (TMF), defined as the sum of the muscle fatigues at each time increment. Based on our results, as well as on the research of others (e.g., Neptune & Hull, in press; Zajac & Winters, 1990), we contend that the minimum muscle fatigue framework presented in the target article does not adequately explain the way the nervous system coordinates muscle activation patterns in dynamic tasks. Furthermore, our results illustrate that the SO methodology of the target article is insufficient for elucidating the general principles of muscle coordination. (For a thorough discussion of the limitations of inverse-dynamics-based approaches, see Zajac, 1993).

Forward dynamics–based test of minimum fatigue during cycling. Neptune and Hull (in press) recently presented dynamic optimization analyses of submaximal steady-state cycling that suggest that experimentally observed joint moments do not minimize the total muscle fatigue over the entire pedaling movement. The muscle excitation patterns responsible for the observed experimental data (kinematics, kinetics, EMG of pedaling at 90 rpm) were estimated using optimal tracking. This involved finding the pattern that, when applied to a forward-dynamics-based biomechanical model of pedaling (including muscle force-length, -velocity, and -activation relationships), resulted in the simulation that best fit the experimental data. Then the total muscle fatigue associated with this muscle excitation pattern was calculated. (Note that they used a slightly different measure than TMF.) However, it was possible to find other muscle excitation patterns that also resulted in successful pedaling simulations but that incurred substantially less total muscle fatigue.

We specifically tested the minimum muscle fatigue hypothesis proposed in the target article by performing a dynamic optimization analysis to determine the coordination pattern (muscle excitations and joint moments) that minimized total muscle fatigue.

Minimum muscle fatigue does not explain coordination of cycling. Similar to Neptune and Hull (in press), the dynamic optimization analysis revealed that observed TMF (calculated from the optimal tracking simulation) could theoretically be reduced by 77% by altering the coordination pattern (minimum TMF simulation) to do relatively more mechanical work in the downstroke. Figure 1 compares the joint moments and pedal forces from the experimental data, the optimal tracking simulation, and the minimum TMF simulation. Of special note are three main points: (a) the optimal tracking simulation joint moments are qualitatively similar to those commonly reported in the cycling literature (e.g., Gregor et al., 1991), (b) the pedal forces in the TMF simulation contain large radially directed components that were not observed experimentally, and (c) the TMF simulation produced more downstroke work and less upstroke work. While the specific details of our analysis (i.e., the precise numbers and curves, the sensitivity of the results to variations in model parameters, and the cost function) may be open to challenge, it cannot be denied that the dynamic optimization approach suggested implications of minimizing muscle fatigue that could not have been ascertained with the SO approach.

Dynamic optimization yields results that cannot be found with SO approach. First, the coordination pattern that minimized the TMF cost over the whole cycle required shifting external mechanical work production from a later portion of the task to an earlier portion (Figure 1). Such a trade-off is possible because the forwards-dynamics-based approach accounts for the future consequences of a change in muscle excitation on the task performance. Since the SO approach evaluates each instant independently, it could not have predicted this solution. Second, optimal simulations often result in coordination patterns, which greatly alter other variables of possible importance to the nervous system that were not included in the cost function. For example, our optimal simulation shows that subjects would have to increase greatly radial pedal forces to minimize TMF cost. The fact that these large radial forces are not seen experimentally may mean that part of the cyclists' strategy is to avoid large radial forces, perhaps to reduce excessive joint loading (which has been hypothesized as a potentially influential criteria for

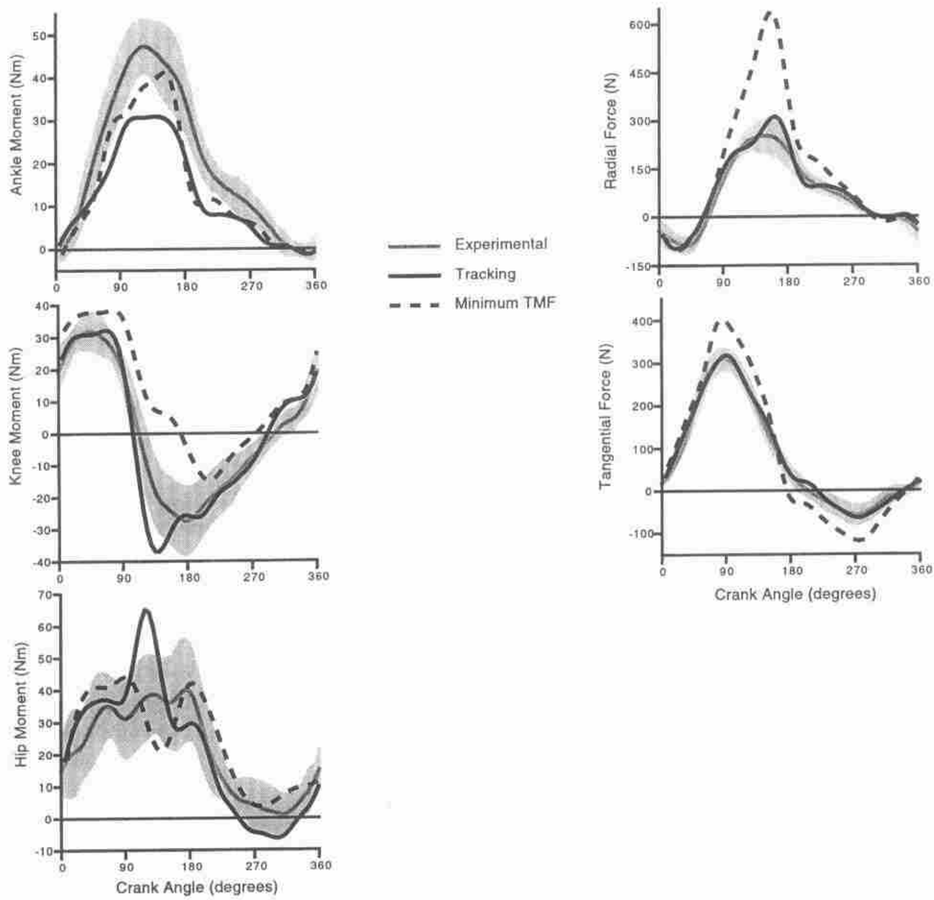

Figure 1 — Joint moments (extensor > 0), tangential pedal forces (perpendicular to crank, propulsive > 0), and radial pedal forces (parallel to crank, compressive < 0) for experimental data (shading equals ± 2 standard deviations), optimal tracking simulation, and minimum TMF simulation. Crank angle zero reference is top-dead-center.

coordination; Zajac & Winters, 1990). These types of inherent dynamic implications of a cost function cannot be evaluated with the SO approach (Zajac, 1993).

In summary, the SO approach cannot test whether the observed joint moments are consistent with minimization of muscle fatigue by the nervous system when a dynamic task is considered in its entirety. Furthermore, the above example shows that the coordination patterns that would minimize TMF in cycling are quite different than those observed experimentally. This strongly suggests that the nervous system's strategy in cycling is not merely to minimize total muscle fatigue.

Our Views

Is muscle coordination predicted by minimum muscle fatigue? Not likely. We believe that our dynamic optimization analysis example for cycling, as well as the results of Neptune and Hull (in press), clearly illustrate that total muscle fatigue does not predict the muscle coordination observed in cycling. Furthermore, it is possible, even likely, that total muscle fatigue was not absolutely minimized in any of the other dynamic tasks investigated using the SO approach in the target article. We believe that the minimum muscle fatigue hypothesis has not been tested sufficiently to serve as a theoretical basis for coordination principles. Similarly, a recent thorough review of force sharing among synergistic muscles concluded that previous efforts to make minimizing fatigue a detailed paradigm of force sharing during normal movements are insufficient (Herzog, 1996).

Does muscle fatigue influence coordination? Most likely. The work of Neptune and Hull (in press) suggests that fatigue is an important factor in predicting preferred cadence during cycling. We believe that avoiding excessive fatigue is an important consideration of the nervous system.

Can minimum muscle fatigue predict synergistic force sharing for a given task performance? Maybe qualitatively. We concede that minimizing muscle fatigue using the SO approach may predict muscle forces that are qualitatively consistent with the observed muscle activity in some, or even many, dynamic tasks. Nevertheless, we are not optimistic that significant quantitative insight will result from the SO approach. For example, we feel that the forces predicted for walking did not match the EMG data very well (Figure 6 in the target article), as the force and EMG magnitudes were very dissimilar for 5 of 7 muscles (e.g., GLM force prediction of 25% and EMG measurement of 90%), and the timing was poorly matched for the two-joint RF. We believe that quantitative insight is necessary for investigating coordination.

Can inverse-dynamics-based analyses explain general muscle coordination principles? No. Insight into general coordination principles requires the ability to *quantitatively* relate muscle force to performance of the task (Zajac, 1993). Further, misleading results can occur if the fundamental mechanical properties of muscles are not considered when general coordination principles are being investigated. Thus, forward dynamics models that include the fundamental mechanical properties of muscles are required. We feel that it is potentially misleading to use inverse-dynamics-based analysis approaches in order to establish general coordination principles. The best that can be done with such an approach is to make descriptive correlations between EMG and joint moments. It is not possible to either explain why a particular muscle is excited or understand the consequences of a particular coordination strategy. Stating that a muscle is excited because it produces the desired combination of joint moments (i.e., RF producing hip flexion and knee extension) is merely begging the real question: Why is the desired combination of joint moments needed at that instant, as opposed to earlier or later?

Should muscle coordination be defined in terms of joint moment demands? No. We believe that general principles of muscle coordination can only be elucidated by defining *how* individual muscle forces contribute to the successful performance of different tasks. We object to the contention that the primary goal of the nervous system is to activate muscles to produce a "given combinations of joint moments." We believe that little insight can result from a coordination principle that requires a motor task to be defined as in Figure 7 of the target article: "Let a motor task be the simultaneous production of an extension moment of 20 N at joint 1 and a flexion moment of –20 N at joint 2." We believe instead that the goal is to activate muscles to perform a given task. We, therefore, heartily disagree with the target article that the elegant concept of task-dependent muscle activation proposed by Loeb (1985) may be "refined as moment-demand-dependent activation." Such an awkward redefinition of coordination is the result of an inverse-dynamics-based approach that is unable to relate joint moments to task performance.

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