ARTICLE

Deconstructing Neurobiological Coordination: The Role of the Biomechanics-Motor Control Nexus

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DAVIDS, K. and P. GLAZIER. Deconstructing neurobiological coordination: the role of the biomechanics-motor control nexus. *Exerc. Sport Sci. Rev.*, Vol. 38, No. 2, pp. 86–90, 2010. *Inherent indeterminacy of neurobiological systems has been revealed by research on coordination of multiarticular actions. We consider three important issues that these investigations raise for biomechanical measurement and performance modeling. These issues highlight the role of dynamic systems theory as a platform for integration of motor control and biomechanics in exercise and sports science.* **Key Words:** movement patterning, nonlinear dynamics, multiarticular actions, degeneracy, indeterminacy, functional variability

INTRODUCTION

In this article, we discuss implications of the insufficient contact between biomechanics and theoretical frameworks in biology, psychology, behavioral neurosciences, and motor control. There have been rare exceptions to this trend, such as work by Patla (25) on the roles of vision in regulating gait and posture, and van Emmerik and coworkers (31) studying the relationship between coordination variability and injury from a dynamic systems perspective. Here, we propose how dynamic systems theory can provide a powerful multidimensional framework to facilitate collaborative interactions between motor control and biomechanics in studying neurobiological coordination. We highlight data from our studies of multiarticular actions to demonstrate how dynamic systems theory could scaffold future work between biomechanists and motor control theorists (6,31), particularly influencing research designs, methods and analysis, and computer simulations in biomechanics (11,33).

Bernstein (2) characterized neurobiological coordination as the process of incorporating redundant motor system degrees of freedom into a controllable unit, requiring the study of movement models that allow this feature to be expressed. Our group's research on coordination and control of multiarticular actions such as kicking (4–6), throwing (26), and hitting (18) has exemplified Bernstein's ideas, showing how individuals functionally (re)organize abundant motor system degrees of freedom to attain movement goals. Our studies of neurobiological coordination have highlighted changes in higher-order kinematic variables relative to performance outcome measures, illustrating how individuals, regardless of skill level, adapt coordination patterns during task performance. This work has exemplified how inherent properties of dynamic neurobiological systems, such as abundance of motor system degrees of freedom and degeneracy, can be exploited to satisfy interacting constraints during learning and performance (26). The data have supported reconceptualization of movement variability in dynamic systems theory as having a more functional role, rather than the traditional interpretation as a source of system error (27).

Our findings have revealed insights relevant for contemporary issues and challenges facing biomechanists studying neurobiological coordination. Thus, based on our research (*e.g.*, Chow *et al.* (5,6), Hristovski *et al.* (18), and Rein *et al.* (26)) and others (*e.g.*, Vaughan (32)), we propose a more theoretically oriented character for biomechanics in the future: (i) to focus hypothesis-driven research on key theoretical issues; (ii) to maintain a balance between methodology development and contributing to theorizing on neurobiological coordination; (iii) and to encourage a more collaborative integration with other relevant scientific subdisciplines such as behavioral neurosciences, psychology, and motor control.

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FOCUSING HYPOTHESIS-DRIVEN RESEARCH IN BIOMECHANICS

Some (*e.g.*, Gregor (13)) have argued that the development of hypothesis-driven research must be prioritized in biomechanics to provide new neurobiological insights. Others (*e.g.*, Winter (35)) have suggested that formal hypotheses have limited value in biomechanics research because of the complexity of neurobiological systems and associated difficulties in accurately predicting motor behavior. However, that stance might have been attributable, in the past, to the lack of an appropriate theoretical framework to capture complexities of neurobiological coordination. Because dynamic systems theory has gained prominence as a framework for studying coordination of multiarticular actions, we have highlighted how inherent indeterminacy of neurobiological systems can be exploited for functional forms of movement variability (*e.g.*, Glazier and Davids (11,12)).

Some biomechanists may have accepted a stronger rationale for hypothesis testing in biomechanics and motor control if adopting dynamic systems theory as an explanatory platform for previous research. For example, in observing stable joint trajectories, Winter (34) reported significant within-participant variability in net moments of force at the knee and hip during gait. This type of variability was interpreted as being compensatory because net moments of force at the hip and knee were allowed to covary, enabling the net extensor pattern or total support moment (the algebraic sum of the net moments of force at the hip, knee, and ankle) to be maintained. He reasoned that covariations between these joints enabled participants to produce consistent joint trajectories, even if erroneous net moments of force were introduced at individual joints. These results are entirely harmonious with insights from dynamic systems theory, revealing how variability in kinematic and temporal gait parameters has a stochastic, rather than a purely deterministic, structure, affording neurobiological systems great flexibility and adaptability (*e.g.*, Riley and Turvey (27)).

Winter (35) also suggested that an insightful approach studying movement behavior might be for investigators to "perturb certain obvious variables and see what changes result," (p. 277) an approach entirely consistent with the experimental strategy of hypothesis testing exemplified by Kelso and Schöner (20). Their coordination dynamics approach advocated the scaling of nonspecific "control" parameters (variables that can alter system organizational states) and observing changes in "order" parameters (collective variables that capture organizational states). This strategy has provided effective insights into inherent self-organizing processes within and between levels of complex neurobiological systems (28) and could provide a useful experimental paradigm for biomechanists. Our research has recently provided hypothesis-driven observations of these insights in coordination of multiarticular actions, typical of sport environments (*e.g.*, Rein *et al.* (26)).

The research strategy outlined by Kelso and colleagues (*e.g.*, (20)) also can alleviate the subsidiary problem of statistical testing of the null hypothesis in biomechanics and motor control research. Because independent variables need to be represented by single data points, biomechanical time series data are often collapsed, to support group mean difference tests or relationship tests to be implemented. We have argued that a problem with reducing biomechanical time series data is that little information is provided on emergent coordination and control processes from which specific performance outcomes emerge (33). We have summarized how applications of nonlinear dynamics to neurobiological coordination have led to the development of analytical tools and techniques enabling multiple time continuous data sets to be analyzed simultaneously, especially in studying emergence of unique movement solutions from individuals in satisfying interacting personal and task constraints. Performance of multiarticular actions in sports can now be examined more fully, both qualitatively (topology) and, as we have pointed out, quantitatively (*e.g.*, Wheat and Glazier (33)) to provide a fine-grained analysis of coordination processes.

TO MAINTAIN A BALANCE BETWEEN METHODOLOGY DEVELOPMENT AND CONTRIBUTING TO THEORIES OF NEUROBIOLOGICAL COORDINATION

Biomechanics research has traditionally been criticized for being somewhat atheoretical and overly preoccupied with methodological development (*e.g.*, Gregor (13) and Norman (24)). One solution to these perceived problems is to base undergraduate biomechanics teaching on a "top down" rather than "bottom up" approach, with students being initially taught theory underpinning biomechanics before focusing on methodological concerns (13). This strategy counters the prevailing perception that biomechanics is merely a descriptive science, lacking a strong theoretical rationale, despite arguments that universal principles of biomechanics are firmly based on the well-substantiated laws of Newtonian, Hamiltonian, and Lagrangian mechanics (*e.g.*, Norman (24)).

For example, in inverse dynamics analyses, algebraic equations, derived from Newton and Euler mechanics, combined with a link-segment model of the human body, are used to calculate joint torques and reaction forces, mechanical work and power transfers from kinematic data, and individual-specific anthropometric (geometric and inertial) parameters for torso and limb segments acting as inputs. Whereas kinematic analyses *describe* motions of limbs and torso, kinetic analyses have the advantage of also *explaining* causes of the observed motions. Hatze (15–17) drew attention to several operational and methodological issues with inverse dynamics analyses, including the adequate complexity of models of the neuromusculoskeletal system.

However, examining adherence to mathematical laws in biomechanics research, although important, is not the same as harnessing fundamental theoretical insights from physics, biology, and psychology to explain neurobiological coordination. Inverse dynamics analyses contain a number of limitations and are still comparatively rare, particularly in sports biomechanics. For example, in a simple leg extension exercise, only the resultant moment of force about the knee can be calculated, not the respective contribution of the hamstring/quadriceps muscle groups. In addition, the contribution to the common output of a particular muscle within a muscle complex cannot be established. This limitation has impeded theoretical understanding of the function of coordinative structures in goal-directed behavior, which we have investigated (*e.g.*, Chow *et al.* (4–6)). We have described this weakness as the problem of measurement indeterminacy (13). Neurobiological indeterminacy is overcome in inverse dynamics analyses by imposing modeling constraints to simplify formal analyses (*e.g.*, Hatze (16)). Because of the risk of oversimplification, a better modeling solution to work toward in the future is to resolve measurement indeterminacy by establishing more of the unknowns (*i.e.*, individual muscle forces).

Although not conceptualized as such, another major concern for Hatze (16) was the inherent indeterminacy of neurobiological systems, a key property that we have investigated in our studies of multiarticular actions (*e.g.*, Hristovski *et al.* (18) and Rein *et al.* (26)). These investigations have revealed that skilled and less skilled individuals can assemble varied movement patterns as functional solutions for achieving specific task goals, ideas that fit the data of Hatze. He considered that myoskeletal inverse dynamics and myocybernetic control inverse problems — the problems of finding net joint torques from experimental observables and the corresponding neural controls, respectively — belonged to a class of "incorrectly" or "ill-posed" problems that by definition did not possess a unique solution. Latash (22) has advanced these ideas, claiming that the problem of inverse dynamics was "worse-than-ill-posed" because information pertaining to one level of the system is used to predict a deterministic solution at another level of the system, despite the inherently stochastic behavior of neurobiological systems.

Fundamental neurobiological indeterminacy exists because there are more system degrees of freedom than strictly needed to successfully perform a specific motor task. A strict mathematical definition of indeterminacy signifies that there are more unknowns than the number of equations that define a system's trajectory.

Computer simulations reported by Hatze (16) demonstrated the extent of indeterminacy at the level of musculo-articular links because, at least for some motions, individual muscle moments may be considerably perturbed without significantly affecting observable motions of the torso and limbs. This "hyposensitivity phenomenon" seems to be even more prominent at the neuromuscular level of analysis, where comparatively chaotic neural control inputs were still able to produce highly coordinated movement patterns. Similar observations were made in the weighted boot study of Hatze (15), where measured (near optimal) and simulated (optimal) limb movements during kicking were almost identical despite being produced by different muscle activation patterns. Indeed, considerably varying neuromuscular activity during the iterative performance of the same motor skill, under similar environmental conditions, has been shown repeatedly in electromyographic studies (8), demonstrating neurobiological degeneracy and the capacity to produce desired outcomes via a multitude of different muscle activation patterns (a concept known in motor behavior by the terms *equifinality* or *sensorimotor equivalence*). Data from research on multiarticular actions have supported these assertions (*e.g.*, Chow *et al.* (6) and Rein *et al.* (26)). For example, we found that both skilled and unskilled participants were able to vary patterns of movement coordination in achieving the same task outcome, in this case, kicking a ball over a barrier to a target (4–6).

Our findings have clearly demonstrated how the proliferation of degrees of freedom affords the neurobiological system's tremendous flexibility and stability when confronted by continuously fluctuating task demands and environmental perturbations of dynamic performance contexts (*e.g.*, Chow *et al.* (4–6), Rein *et al.* (26), and van Emmerik *et al.* (31)). The results are harmonious with ideas from theoretical biology, proposing that the term *degeneracy* is more appropriate than *redundancy* in analyses of functional behavior in neurobiological systems (*e.g.*, Edelman and Galy (9)). It has been argued that redundancy should be reserved for the study of electronic or mechanical systems, where duplication or repetition of *identical* system components is an important design feature that provides backup in case of system failure. In neurobiological systems, degeneracy is a more suitable descriptor as system components that are structurally *different* that can still produce *similar* or *different* functions or lead to *similar* or *different* outputs depending on context. Inherent neurobiological flexibility in achieving performance outcomes is not just a feature of the *number* of available motor system degrees of freedom (captured by system redundancy) but also the *role* of these microcomponents in assembling actions (captured by system degeneracy).

Although an abundance of degrees of freedom may be considered a "blessing" for a neurobiological system to assemble movement solutions for sensorimotor task performance, they pose a regulatory problem for the central nervous system. The dimensionality, and the control problem for the central nervous system, can effectively be reduced by formation of functional synergies (2) or coordinative structures (21). These structural units emerge from inherent processes of self-organization ubiquitous in complex neurobiological systems and constraints that limit and define the operational boundaries of the neurobiological system (19,21). A distinguishing feature of these task-specific devices is that if one of the components introduces an error into the common output, other components automatically make compensatory adjustments to minimize error effects (23). A good example of synergy or a coordinative structure, discussed earlier in this article, is the net extensor pattern or total support moment described by Winter (35), but many more examples exist at various levels of the neuromusculoskeletal system.

For biomechanists, the issue of indeterminacy has been viewed as a perennial problem and significant barrier to progress (32). Because there is currently no way of determining individual muscle forces without *in vivo* transducers, one method used by biomechanists in modeling is to circumvent the problem of too many unknowns by reducing all muscle, bone, and ligament forces crossing a joint to a single vector. Although mathematically convenient, this approach has several limitations, which restrict the use of inverse dynamics analyses. For example, the calculation of a resultant or net joint torque provides no information regarding antagonistic muscle activity and precludes the partitioning of forces among individual muscles that comprise a specific muscle group. Latash (22) argued that the myoskeletal inverse dynamics problem and the related myocybernetic control inverse problem "cannot be unambiguously solved, regardless of the quantity and quality of available information [...] they should be either reformulated or totally abandoned" (p. 298). However, in the case of the myoskeletal inverse dynamics problem, reformulation to reduce the number of unknowns has compromised the effectiveness and applicability of inverse dynamics analyses, rendering the net joint torque a rather abstract concept of limited practical relevance. Overlooking the fact that they are inherently unreliable quantities (16), net joint torques provide little or no more information about motor synergies or coordinative structures other than the insights of Winter (35). Even if more unknowns could be calculated, as noted earlier, the inherent stochasticity of neurobiological systems signifies that production of a particular set of muscle forces or recruitment of a particular set of motor units is difficult to predict, shaped by the confluence of constraints on performance. As Latash (22) observed, the central nervous system "does not care" how various degrees of freedom at different levels of the neurobiological system coalesce during movement coordination as long as the trajectory of the end-effector is preserved and performance goals are attained.

Although current evidence on the relative value of inverse dynamics analyses altogether is inconclusive, a shift of emphasis seems most appropriate given that neurobiological systems do not seem to be particularly amenable to theoretical or experimental analyses from the standpoint of traditional mechanics. As we have highlighted, concepts from dynamic systems theory represent an alternative platform on which to base further research endeavor in biomechanics and motor control (11,12). The concepts and analytical tools and techniques of dynamic systems theory have the potential to enable biomechanists, working collaboratively with motor control theorists, to *measure*, *explain*, and *predict* how stability, variability, and transitions among system coordinative states at the kinematic level of analysis might be functional. In addition to providing the theoretical foundation for the "top down" approach advocated by Gregor (13), conceptualizing neurobiological systems as complex nonlinear dynamic systems also could provide the basis for "interdisciplinary vertical integration" and for "cross training" exercise and sports science graduate students to underpin future research endeavor in biomechanics.

A UNIFYING THEORETICAL FRAMEWORK: THE KEY TO INTERDISCIPLINARY RESEARCH SUCCESS?

The need for greater interdisciplinarity has been a reoccurring theme in exercise and sports science. However, despite the rhetoric genuine interdisciplinary research, where a group of scientists collaborate in an effort to *integrate* their specific domains of expertise to extend knowledge on performance, has been the exception rather than the rule. We and others have proposed the collaboration of biomechanists and motor control theorists as having significant potential (*e.g.*, Glazier and Davids (11) and van Emmerik *et al.* (31)). However, for a more effective working partnership to emerge in a motor control–biomechanics nexus, powerful theoretical frameworks are needed. Cross training of graduate students in different disciplines, as suggested by Gregor (13), will benefit from the adoption of strong theoretical insights to provide sufficient rationale for forging meaningful, sustainable, and productive interdisciplinary collaborations.

It has been suggested that "vertical integration" might provide the foundation and much needed impetus for interdisciplinary collaboration, not only between biomechanists and motor control theorists, but also scientists from other disciplines (13). This approach is captured in the phrase "molecules to movement." Gregor (13) proposed that "laws that govern the interaction of protein molecules (*i.e.*, systems biology) might someday be applied to the integrated interaction of physiological systems involved in movement control" (p. 37), but did not indicate how this interaction might be understood. This integrated approach can avoid reductionism by adopting a systems-oriented approach as a relevant theoretical framework. Key theoretical concepts from dynamic systems theory, such as physical self-organization and constraints, can feature prominently in a biomechanics–motor control nexus dedicated to the discovery and application of these laws of interaction. A compelling attribute of dynamic systems theory is that the same principles can be used to explain organization at different levels of a complex system, irrespective of its material composition (14). For example, processes of self-organization and constraints have been used to explain stability, variability, and transitions at different levels of neurobiological system organization including cellular, molecular, neuronal, and musculoskeletal. The universal applicability of dynamic systems theory principles and concepts, such as the role of self-organization and pattern-forming dynamics under constraints, could provide a sound basis for understanding how "vertical integration" might be achieved in the study of neurobiological coordination.

A number of investigations have already attempted to examine coupling between different levels of complex neurobiological systems, exemplified in studies of locomotor-respiratory coupling in a variety of motor tasks, including cycling (1), running (3), and rowing (7,29). St. Clair Gibson and Noakes (30) also provided a holistic multilevel approach to the study of fatigue based on dynamic systems theory. Their empirical findings are consistent with findings in our program of work (*e.g.*, Chow *et al.* (4–6), Hristovski *et al.* (18), Rein *et al.* (26)), in which we showed that small-scale fluctuations at a microscopic level of the system (*e.g.*, changes at the neuromuscular levels) can lead to large-scale qualitative and quantitative changes observable at a more macroscopic level (*e.g.*, changes in movement coordination leading to variations in task performance). The results of our studies demonstrate the potential of "vertical integration" to provide a more complete understanding of normal and pathological functioning in neurobiological systems, exemplifying how biomechanists, in collaboration with scientists from other disciplines, might continue to adopt this research strategy in the future.

CONCLUSIONS

The nexus between motor control and biomechanics has the potential to enhance the understanding of neurobiological coordination. However, we have argued that this collaborative relationship needs a powerful theoretical framework, such as dynamic systems theory, to cope with neurobiological system indeterminacy. Although support for this theoretical framework in the human movement sciences is still growing with questions remaining on its explanatory power, here we have discussed how it might provide a valid platform to resolve some of the most pressing issues facing contemporary biomechanics.

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