

A Commentary on Latash: “Useful and Useless Misnomers in Motor Control”

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As Latash correctly points out (Latash, 2024), imprecise language in Science in general, and the motor control field in particular, is unfortunate when it arises as it can hinder our understanding. It goes without saying that scientists do not intend to be imprecise. Rather, we believe this is a risk we run in the course of our well-intentioned and arduous efforts to integrate across disparate disciplines. At times, these efforts lead to an imperfect capturing of complex biological principles as reductionist mathematical terms or, conversely, the use of clear mathematical concepts as metaphors when extrapolating them to biological sciences. As an example of the former, skeletal articulations are not the mechanical hinges that we so conveniently use in rigid body mechanics (Valero-Cuevas, 2015). As to the latter, the term “optimization” has a clear meaning that drives specific numerical methods, but no one will agree absolutely that biological systems always optimize in the engineering sense (i.e., by finding a global minimum for a unique, universal and preferably quadratic, cost function; Cohn et al., 2018).

Thus, our goal as scientists should be to use the best possible terms at the time (given that language evolves continually) to reach a useful understanding of neuromuscular systems—and continue to challenge and refine our language as that understanding grows. Epistemologically speaking, our concepts in motor control are our best current models of biological systems. Yet, to paraphrase George Box, all models are wrong but some are useful. Let us work toward making our language useful.

Synergies

In that same spirit, we would like to highlight some refinements to the notion of “synergies” over the past few years. Putting aside the well-defined notion of pathologic synergies that arise in some neurological conditions such as stroke (Dewald et al., 1995), synergies in neurotypical animals and humans are invoked as a broad class of strategies to control multiple muscles, and even “simplify” their control (Cheung & Seki, 2021; Cohn et al., 2018; Kutch & Valero-Cuevas, 2012;

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Loeb, 2021 and references therein). Since the initial numerical description of nonpathologic movement synergies using principal components analysis by Santello et al. (1998), there have been several nuanced refinements of the term synergies.

Descriptive Versus Prescriptive Synergies

When using dimensionality reduction techniques to extract basis functions (i.e., synergies) from experimental data like muscle activities, joint angle, and so on, it is their interpretation that is critical. These synergies can be “descriptive” if what they capture are patterns in the experimental data that reflect the fact that motor actions naturally occur within a lower dimensional structure given by the constraints of the body and task. That is, the mechanical capabilities of a limb and the constraints defining a task define a set of feasible motor actions. This feasible activation set is the landscape within which all motor learning, performance, and adaptation must occur (Valero-Cuevas, 2015). Thus, any successful execution of a task must, by construction, inhabit a lower dimensional set that can be *described* by “few” basis functions. These are empirical observations, numerically describing the inherent structure of motor behavior under task constraints. Said differently, it is to be expected that analysis of behavior will detect correlations (i.e., lower dimensional structure), as a consequence of successful executions of the given task (Brock & Valero-Cuevas, 2016).

In contrast, “prescriptive” synergies are strategies implemented by the controller to perform a task, meaning that the control law explicitly imposes coordination of muscle actions to inhabit and traverse the feasible activation set. Experimentally detected correlations in the data are, by construction, descriptive synergies. For these correlations to rise to the status of prescriptive synergies, one must demonstrate that the correlations detected are a direct consequence of a control law, or identify the neural substrates that produce them (Brock & Valero-Cuevas, 2016; Cheung & Seki, 2021; d’Avella & Pai, 2010; Kutch & Valero-Cuevas, 2012; Mulla & Keir, 2023).

Coarse Versus Fine Synergies

When extracting descriptive or prescriptive synergies, the investigator is faced with an unavoidable choice: How far does one press dimensionality reduction by explicitly stating that one will consider only those synergies needed to explain a sufficient percent of the variance (80%, 90%, 95%) in the data. The implicit (or explicit) assumption is that only those “coarse synergies” capture the salient features of the lower dimensional structure in the data (Barradas et al., 2020; Bartsch-Jimenez et al., 2023). The remaining variance is either disregarded as uninformative, attributed to noise, or considered irrelevant. However, one can consider the remaining “fine synergies” to represent subtle, yet informative, features of behavior (Bartsch-Jimenez et al., 2023). Other work had also indicated that the remainder is not noise and requires cautious interpretation (Barradas et al., 2020; Loeb, 2021). This echoes the numerical and algorithmic difficulties pointed out by Clewley et al. (2008) about determining the true number of degrees of freedom in motor systems.

Underdetermined Versus Overdetermined System

The literature in motor control is dominated by the mathematically correct notion of muscle redundancy for net (i.e., total) torque production: an infinite number of muscle forces can produce the same net joint torque about a joint. This applies to the case of the simple agonist–antagonist pair of muscles and is exacerbated as more muscles are added. This underdetermined problem (i.e., more variables than equations) gives rise to the so-called “central problem of motor control” (Latash, 2012 and references therein). However, an equally important—but less well-known—problem arises when considering the inevitable effect joint rotations have on musculotendon excursions (i.e., lengthening or shortening). This is an overdetermined problem where a single joint rotation produces excursions in all musculotendons that cross it (i.e., more equations than variables) which, at most, has one solution (Hagen & Valero-Cuevas, 2017; Mulla & Keir, 2023; Niyo et al., 2024; Valero-Cuevas, 2015). Here, the neural controller must ensure that all musculotendon excursions keep up with the joint rotation (or at the very least those in the lengthening musculotendons; as shortening muscles can go slack). That is, the failure of *any* lengthening musculotendon to keep up with the joint rotation will cause the joint rotation (and by extension the limb movement) to be disrupted or lock up (Hagen & Valero-Cuevas, 2017; Mulla & Keir, 2023; Niyo et al., 2024; Valero-Cuevas, 2015). Why would any musculotendon fail to lengthen as needed? As Sherrington pointed out, afferented muscles produce stretch reflexes driven via muscle spindle Ia and II afferent signals. And in fact, if not properly modulated, they can disrupt or stop joint rotations (Niyo et al., 2024; Sherrington, 1913). This is the opposite of muscle redundancy for the control of limb movement. It is critical then to recognize that controlling a system that is simultaneously underdetermined (from the perspective of muscle activations for net joint torque production) and overdetermined (from the perspective of musculotendon excursions for joint rotations) has profound consequences to our understanding of motor control for naturalistic behavior (Valero-Cuevas, 2015).

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