BJMB
Brazilian Journal of Motor Behavior

Special issue:
"In memory of Michael Turvey"

Mini-review: Biological Movements as Objects of Natural Science

MARK L. LATASH[1]

[1] Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802, USA

Correspondence to: Mark L. Latash
Department of Kinesiology, Rec.Hall-267, The Pennsylvania State University, University Park, PA 16802, USA
tel: (814) 863-5374
email: mll11@psu.edu
https://doi.org/10.20338/bjmb.v17i6.404

HIGHLIGHTS

- Biological movements obey both basic and biology-specific laws of nature;
- Control of movements operates with spatial referent coordinates for the effectors;
- A control hierarchy includes synergies stabilizing salient performance variables;
- This scheme covers actions from individual motor unit to the whole body.

ABBREVIATIONS

a	Acceleration
C	Coactivation
CNS	Central nervous system
EMG	Electromyographic
F	Force
m	Mass
M-modes	Muscle modes
MU	Motor units
MU-modes	Robust MU groups
R	Reciprocal
RC	Referent coordinate
UCM	Uncontrolled manifold

PUBLICATION DATA
Received 16 11 2023
Accepted 26 11 2023
Published 22 12 2023

BACKGROUND: Two approaches to biological movement have dominated the field, the computational approach (internal models) and the approach based on laws of nature pioneered by several researchers including Michael Turvey.
AIM AND METHOD: We review a body of literature exploring and expanding the approach based on laws of nature. We show, in particular, how this approach fits the philosophical traditions of Merleau-Ponty, the theory of control with spatial referent coordinates, the principle of abundance, and the concept of performance-stabilizing synergies using the uncontrolled manifold hypothesis.
RESULTS: Currently, this scheme of motor control has been applied successfully in studies of a variety of effectors, from single motor units to the whole body, a variety of tasks, and various populations. It led to the discovery of new phenomena and new interpretations of known phenomena. It has been productive in studies of neurological patients offering new understanding of some of the common pathologies (e.g., spasticity) and new tools for early diagnosis of various subcortical disorders and monitoring treatment effects.
CONCLUSION: Currently, this field faces a number of challenges including the following: Mapping steps in the hierarchical control scheme on neurophysiological structures and circuits, understanding the relative role of intra-muscle (spinal) and multi-effector (supraspinal) synergies, expanding studies of movements in intact animals and animal preparation, and moving beyond the current scheme to fields traditionally associated with psychology. Just like the current scheme represents moving "outside the box" of classical mechanics, a step outside the current thinking is needed.

KEYWORDS: Law of nature | Referent coordinate | Uncontrolled manifold | Synergy | Hierarchy

INTRODUCTION

Two approaches have dominated the field of movement studies over the past half-a-century. One of them assumes computations performed by certain structures within the central nervous system (CNS) to solve problems associated with complex interactions among body structures, effects of reflex feedback loops on muscle activation, muscle force-length and force-velocity properties, interactions with the environment, and time delays during information transmission along neural fibers. These computations have been assumed to be performed by hypothetical neural structures commonly addressed as internal models (reviewed by Shadmehr and Wise [1]). This approach can be traced back to the control theory and ideas of programming peripheral movement patterns by the CNS, mechanical or electromyographic, in particular the generalized motor program, the dual-strategy hypothesis, the pulse-step hypothesis, and a number of related ideas [2,3].

The alternative approach views the CNS not as a computational device, but as a natural object that behaves according to laws of nature, some of which are known to researchers – basic laws of classical physics that apply equally to biological and inanimate objects – and others that may be specific for living systems. This approach has been summarized in a classical book by Peter Kugler and Michael Turvey [4] showing how complex behavioral patterns can emerge from interactions within a limited set of elements acting according to relatively simple local rules. This approach follows the traditions of classical physics. Physicists have never assumed

computational processes taking place in their objects of study. Instead, researchers use computational tools to account for the observations and summarize them in a compact way, commonly in the form of equations reflecting laws of nature. Laws of nature link variables salient for the objects of study with the help of parameters. For example, the well-known Second Newton's Law, ***F*** = *m****a***, links two variables, force (***F***) and acceleration (***a***) with the help of a parameter, mass (*m*). Note that variables are constrained by the laws of nature while parameters are not. In particular, a change in force (***F***) leads to a change in ***a*** but not *m*, although, mathematically, ***a*** and *m* are equivalent in the equation: ***F*** = *m****a*** is equivalent to ***F*** = ***a****m*.

While biological objects obey classical laws of physics, these laws only constrain them but do not prescribe their behavior. In particular, animals commonly walk uphill and swim against the current, which is not commonly seen in the inanimate nature. Unlike stones, animals can jump against the field of gravity. But then, just like stones, they fall back to the ground. The unusual behaviors of living objects suggest that these behaviors are reflections of biology-specific laws of nature in addition to the laws of classical physics. One can even define a biological object as an object that can create new relations among salient variables and involving new parameters, i.e., new laws of nature, based on complex chains and clusters of classical laws of physics (reviewed in Latash [5]).

Philosophically, this approach can be traced back to the famous argument between Albert Einstein and Henri Bergson (reviewed in Canales [6]) and views of a French philosopher, Maurice Merleau-Ponty [7], who suggested the existence of separate sets of laws of nature related to the inanimate nature (classical physics), living systems, and systems with consciousness, such as humans. This view has been developed recently [8] based on two actively developed ideas within the field of motor control. The first is the idea of neural control of movements with time changes in spatial referent coordinates (RC) for the effectors organized into a hierarchy (reviewed in [9,10]). The second is the idea of synergies based on the principle of motor abundance [11]: Following traditions set by Bernstein [12,13], synergies are viewed as neural organizations that ensure stability of salient, task-specific variables (reviewed in [5,14,15]). A crucial step in the experimental analysis of synergies has been the introduction of the uncontrolled manifold (UCM) hypothesis [16] and associated computational tools such as analysis of inter-trial variance in subspaces of variables produced by elements and analysis of motor equivalence.

The two ideas have been united into a general scheme on the control of movements illustrated in Fig. 1. The left panel presents the general scheme of a control hierarchy with a sequence of few-to-many mappings operating with referent coordinates for the effectors. The back-coupling from peripheral sensory endings and within the CNS are shown with arrows [17,18,19]. The right panels illustrate RCs at various levels, from individual motor units (MU) to robust MU groups (MU-modes), to muscles, to muscle modes (M-modes), to joint-level control variables (reciprocal and coactivation commands, *R* and *C* commands), and to whole body pairs of {*R*; *C*} commands for each kinematic degree of freedom.

Over the recent years, the ideas and concepts illustrated in Fig. 1 have been used to quantify motor synergies in various spaces, kinetic, kinematic, electromyographic (EMG), and control variables over a variety of tasks, effector sets, and populations (reviewed in [9,15]). They have led to the discovery of a number of novel phenomena such as impairment in the voluntary control of RC within the healthy spatial range after stroke, anticipatory synergy adjustments, and trade-offs between synergies at different levels of a hierarchy, as well as to new interpretations of know phenomena such as the tri-phasic EMG patterns, violations of equifinality, and unintentional drifts in motor performance. In addition, changes in the synergic control with aging, neurological disorder, fatigue, exercise, etc. have been quantified.

In particular, recent studies have demonstrated that individual MUs within a muscle form robust groups – MU-modes – with positive covariation of firing frequencies within a mode, while the gains at MU-mode involvement co-vary across trials negatively to stabilize the force magnitude produced by the muscle in isometric conditions [20]. A number of findings pointed at spinal circuitry as the neural substrate for this organization. In particular, during multi-finger tasks, MU-mode synergies stabilized reflex changes in muscle force, while analysis in the space of finger forces did not show such synergies [21]. On the other hand, effects of dominance have been described for multi-finger synergies but not for multi-MU-mode synergies [22]. At the other end of the spectrum, analysis of performance-stabilizing synergies at the task level using mechanical variables reflecting the *R* and *C* commands has documented such synergies over a range of tasks, from single-finger pressing to whole-body standing [23,24].

Currently, three major issues seem to dominate thinking within the theoretical scheme illustrated in Fig. 1. The first one is related to practical applications of this scheme to such fields as movement disorders, rehabilitation, and training. On the one hand, the idea of impaired control of RC shifts in spasticity following stroke has been developed to suggest both an objective biomarker of spasticity and new methods of rehabilitation [25,26]. On the other hand, studies of impaired indices of stability and ASAs in patients with subcortical motor disorders such as Parkinson's disease, multiple sclerosis, and multi-system brain atrophy have suggested that these indices can be used as sensitive biomarkers for both early diagnosis of these and related disorders and effects of treatment [27]. The fact that changes in these indices can be seen in clinically unaffected parts of the body, in clinically uncompromised tasks, and even in neurologically healthy persons at high risk for subcortical disorders [28] suggests their very high sensitivity to such conditions. The number of studies using these tools and concepts remains small, and there is ample space for new explorations and discoveries.

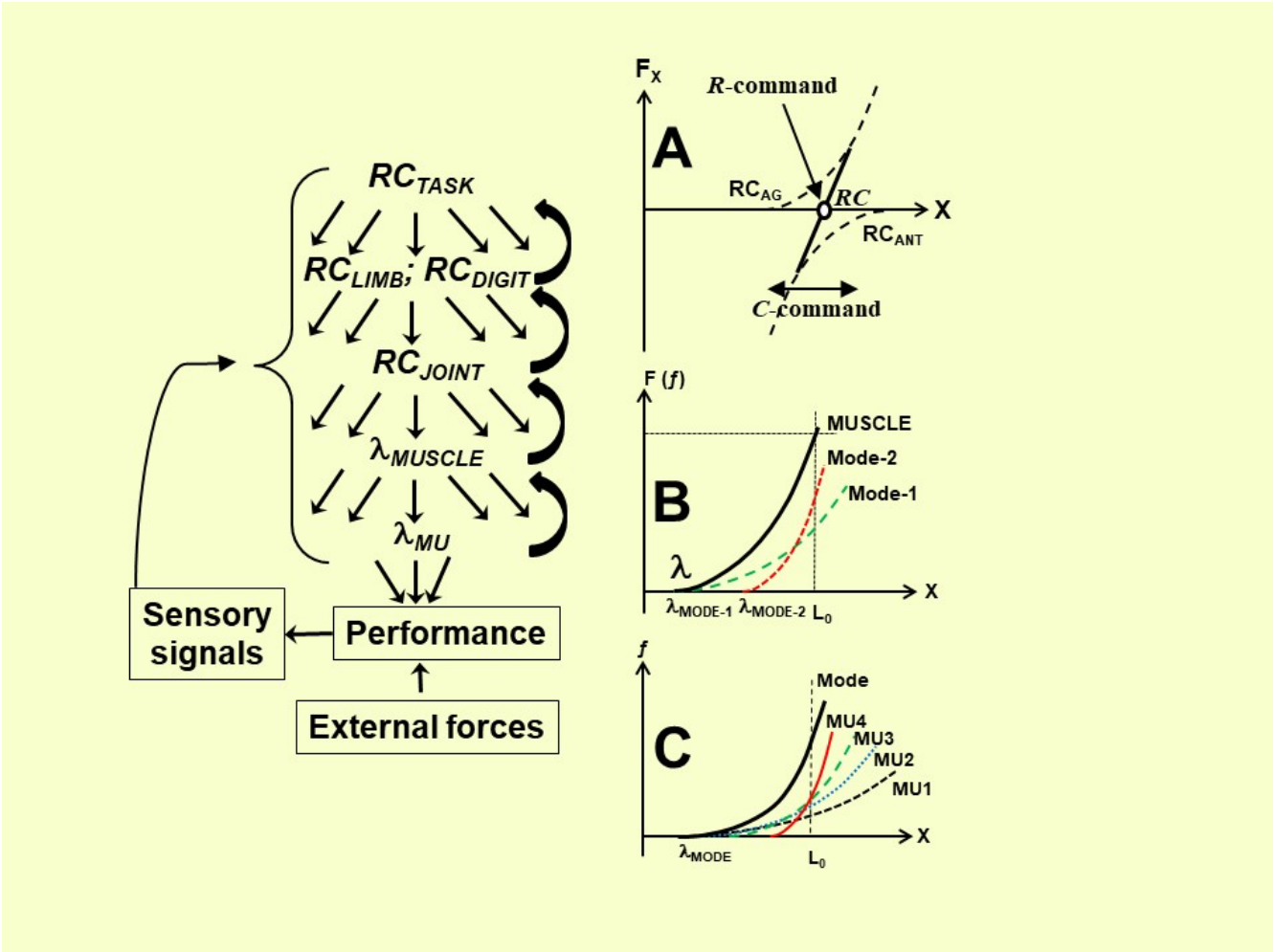

Figure 1. The left panel illustrates schematically a hierarchical scheme involved in the control of voluntary movements. At each level, from the task level (which can involve the whole body) to the levels of involved effectors, muscles and motor units (MU), the control involves specification of spatial referent coordinates (RC; equivalent to the stretch reflex threshold, λ, for muscles and MUs). The back-coupling loops (shown with curved arrows) insure stability of performance. The right panel A shows force-coordinate (F-X) characteristics of the opposing muscle groups (dashed curves) and of the effector (thick line). RC for the agonist and antagonist muscles (RC_{AG} and RC_{ANT}) are set by the controller. Their shifts can be described with two basic commands: reciprocal (R, which defines the RC for the effector) and coactivation (C, which defines the spatial coactivation range). Panel B illustrates how muscle action in isometric conditions (muscle length – L_0) controlled with λ is produced by λs to two robust groups of MUs (MU-modes). Muscle-level λ is stabilized by negative covariation of MU-mode λs. Panel C shows λ for a MU-mode and λs to the contributing MUs, which show positive covariation.

The second group of issues is related to possible neural substrates involved in the hierarchy shown in Fig. 1 and associated performance-stabilizing synergies. The most comprehensive scheme has been developed by the group of Gregor Schöner [18], but the relations of the most important conceptual steps in that scheme to neurophysiological structures and processes remain tentative. The mentioned clinical observations suggest the importance of loops through the basal ganglia and cerebellum for multi-muscle, multi-effector synergies stabilizing task-specific variables. On the other hand, studies of intra-muscle, multi-MU-mode synergies point at spinal circuitry as a major important contributor to synergies. A recent study of force-stabilizing synergies in multi-finger accurate force production tasks before and after turning the visual feedback on the force magnitude off has shown that synergies in both multi-finger space and MU-mode space stabilize force when visual feedback is available. Without visual feedback, however, force shows an unintentional drift to lower magnitudes (cf. [29]) accompanied by disappearance of multi-finger synergies with no effects on MU-mode synergies [30]. These observations support the hypothesis that multi-effector (multi-muscle) synergies are supraspinal in origin while the multi-MU-mode (intra-muscle) synergies are based on spinal circuitry (as summarized in Fig. 2).

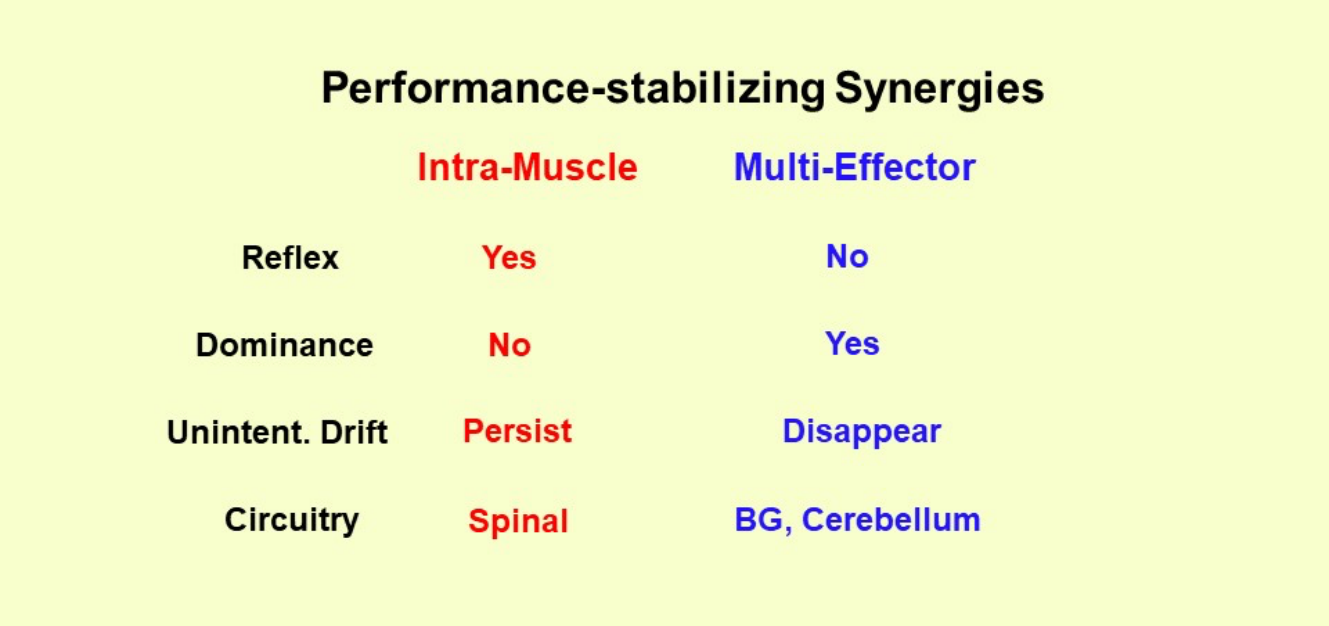

Figure 2. The contrast between intra-muscle and multi-effector (multi-muscle) synergies. The former, but not the latter, stabilize reflex-induced muscle action and persist during unintentional force drifts. The latter, but not the former, show effects of hand dominance. Intra-muscle synergies are likely reflecting action by spinal circuitry. In contrast, multi-effector synergies are likely to depend strongly on action of subcortical loops through the basal ganglia (BG) and cerebellum

So far, only a handful of studies explored performance-stabilizing synergies in animals [31,32]. These studies in intact animals documented such synergies in spaces of individual joint rotations during such functional movements as locomotion and object manipulation. The possibility to perform invasive studies and studies of animal preparations with injuries to specific parts of the central nervous system could be highly valuable for understanding neurophysiological mechanisms involved in the control hierarchy.

The third group of issues is related to inherent limits of the scheme illustrated in Fig. 1. On the one hand, this scheme has been developed to account for phenomena outside the field of neural control of movement, such as aspects of kinesthetic perception [33]. On the other hand, its limitations are also obvious. In particular, where do $RC_{TASK}(t)$ time functions come from? This question remains outside the scope of this scheme and has to be delegated to unidentified "higher levels" dealing with issues commonly covered in the field of psychology. Some aspects of these issues have been addressed in ingenious studies of the group of Michael Turvey, in particular those related to regularities in the relative phase seen during multi-effectors tasks performed both by a single person and by two persons [34]. Other issues, for example those related to target selection, have been addressed within the dynamical field theory developed by Gregor Schöner and colleagues [35,36].

The expression "thinking outside the box" is used frequently with respect to any original idea, even if it is formulated within the circle of ideas and concepts defined by "the box". Michael Turvey and his colleagues thought truly outside the box of classical psychology and motor control by introducing elements of the dynamical theory into these fields [37,38]. In the field of motor control, the original "box" was defined by the Newtonian mechanics reshaped into biomechanics. Its power, well-developed computational apparatus, and numerous successful applications in engineering created an impression that it was equally salient and omnipotent with respect to biological movement. Even in our days, many approaches to motor control start with an assumption that seems unassailable: "To perform a desired movement, the CNS has to send commands generating requisite force patterns." Models of motor control manipulating muscle activation patterns may seem to be "outside the box" of the Newtonian mechanics, but in fact they have not moved far away from it: They still assume that the brain somehow precomputes and prescribes time patterns of peripheral variables to ensure requisite mechanics at individual muscle level.

The equilibrium-point hypothesis [39,40] and its later developments as the control with spatial RCs (reviewed in [9]) was another example of true thinking "outside the box". The idea that accurate movements can be produced by prescribing patterns of parameters within relevant laws of nature, i.e., using parametric control, and that forces emerge just like any other variables, mechanical or EMG, was truly revolutionary. In spite of many attempts to disprove the RC hypothesis coming from the "box" of Newtonian mechanics, the hypothesis has survived, developed, and turned into a respected theory, the only viable theory of motor control (as the author of this paper thinks). One can even say that it has developed into another "box", which has incorporated the Newtonian mechanics but introduced a broader understanding of the specific features of the neural control of biological movement.

Now, the time may be ripe to start moving outside the "RC box" and complement it with a more general understanding of psychological processes leading to the generation of RC(t) at the task level. These will have to unite concepts and ideas from the fields of memory, perception, optimality, and maybe a few others. This is a challenge for the next generation of researchers.

REFERENCES

1. Shadmehr R, Wise SP (2005) *The Computational Neurobiology of Reaching and Pointing*. MIT Press: Cambridge, MA.
2. Gottlieb GL, Corcos DM, Agarwal GC. Strategies for the control of voluntary movements with one mechanical degree of freedom. *Behav Brain Sci. 1989;* 12:189-250.
3. Schmidt RA. A schema theory of discrete motor skill learning. *Psychol Rev.* 1975; 82:225-260.
4. Kugler PN, Turvey MT (1987) *Information, natural law, and the self-assembly of rhythmic movement*. Hillsdale, NJ: Erl
5. Latash ML (2019) *Physics of Biological Action and Perception*. Academic Press: New York, NY.
6. Canales J (2015) *The Physicist and the Philosopher: Einstein, Bergson, and the Debate that Changed Our Understanding of Time*. Princeton University Press: Princeton, NJ.
7. Merleau-Ponty M (1942/1963). *The Structure of Behavior*. (Trans. by A Fisher). Boston: Beacon Press.
8. Kretchmar S, Latash ML. Human movement: In search of borderlands between philosophy and physics. *Kines Rev*. 2022; 11:179-190.
9. Feldman AG (2015) *Referent control of action and perception: Challenging conventional theories in behavioral science*. Springer, NY.
10. Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control.* 2010; 14:294-322.
11. Latash ML. The bliss (not the problem) of motor abundance (not redundancy). *Hum Move Sci.* 2012; 217:1-5.
12. Bernstein NA (1947) *On the Construction of Movements*. Medgiz: Moscow (in Russian). English translation in Latash 2020.
13. Latash ML (Ed.) (2020) *Bernstein's Construction of Movements*. Routledge: Abingdon, UK.
14. Turvey MT. Action and perception at the level of synergies. *Hum Move Sci. 2007;* 26:657-697.
15. Latash ML. One more time about motor (and non-motor) synergies. *Exp Brain Res.* 2021; 239:2951-2967.
16. Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res*. 1999; 126:289-306.
17. Latash ML, Shim JK, Smilga AV, Zatsiorsky V. A central back-coupling hypothesis on the organization of motor synergies: a physical metaphor and a neural model. *Biol Cybern*. 2005; 92:186-191.
18. Martin V, Reimann H, Schöner G. A process account of the uncontrolled manifold structure of joint space variance in pointing movements. *Biol Cybern,* 2019; 113:293-307.
19. Martin V, Scholz JP, Schöner G. Redundancy, self-motion, and motor control. *Neural Comput.* 2009; 21:1371-1414.
20. Madarshahian S, Letizi J, Latash ML. Synergic control of a single muscle: The example of flexor digitorum superficialis. *J Physiol*. 2021; 599:1261-1279.
21. Madarshahian S, Ricotta J, Latash ML. Intra-muscle synergies stabilizing reflex-mediated force changes. *Neurosci.* 2022; 505:59-77.
22. Latash ML, Madarshahian S, Ricotta J. Intra-muscle synergies: Their place in the neural control hierarchy. *Motor Control*. 2023; 27:402-441.
23. Ambike S, Mattos D, Zatsiorsky VM, Latash ML. Synergies in the space of control variables within the equilibrium-point hypothesis. *Neurosci.* 2016; 315:150-161.
24. Nardon M, Pascucci F, Cesari P, Bertucco M, Latash ML. Synergies stabilizing vertical posture in spaces of control variables. *Neurosci.* 2022; 500:79-94.
25. Levin MF, Feldman AG. The role of stretch reflex threshold regulation in normal and impaired motor control. *Brain Res.* 1994; 657:23-30.
26. Turpin NA, Feldman AG, Levin MF. Stretch-reflex threshold modulation during active elbow movements in post-stroke survivors with spasticity. *Clin Neurophysiol*. 2017; 128:1891-1897.
27. Latash ML, Huang X. Neural control of movement stability: Lessons from studies of neurological patients. *Neurosci*. 2015; 301:39-48.
28. Lewis MM, Lee E-Y, Jo HJ, Park J, Latash ML, Huang X. Synergy as a new and sensitive marker of basal ganglia dysfunction: A study of asymptomatic welders. *Neurotoxicol*. 2016; 56:76-85.
29. Vaillancourt DE, Russell DM. Temporal capacity of short-term visuomotor memory in continuous force production. *Exp Brain Res.* 2002; 145:275-285.
30. De SD, Ricotta JM, Benamati A, Latash ML. Two classes of action-stabilizing synergies reflecting spinal and supraspinal circuitry. *J Neurophysiol. 2024*; 131:152-165.
31. Klishko AN, Farrell BJ, Beloozerova IN, Latash ML, Prilutsky BI. Stabilization of cat paw trajectory during locomotion. *J Neurophysiol*. 2014; 112:1376-1391.
32. Mangalam M, Rein R, Fragaszy DM. Bearded Capuchin monkeys use joint strategies to stabilize the hammer trajectory while cracking nuts in bipedal stance. *Proc Biol Sci*. 2018; 285:20181797.
33. Latash ML. Stability of kinesthetic perception in efferent-afferent spaces: The concept of iso-perceptual manifold. *Neurosci.* 2018; 372:97-113.
34. Schmidt RC, Carello C, Turvey MT. Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *J Exp Psychol: Hum Percept Perform*. 1990; 16:227-247.
35. Erlhagen W, Schöner G. Dynamic field theory of movement preparation. *Psychol Rev*. 2002; 109:545-572.
36. Schöner G, Thelen E. Using dynamic field theory to rethink infant habituation. *Psychol Rev*. 2006; 113:273-299.

37. Kelso JAS, Holt KG, Kugler PN, Turvey MT (1980) On the concept of coordinative structures as dissipative structures. II. Empirical lines of convergence. In: Stelmach GE, Requin J (eds.) *Tutorials in Motor Behavior*, pp. 49-70, Amsterdam: N-Holland Publ.
38. Kugler PN, Kelso JAS, & Turvey MT (1980). On the concept of coordinative structures as dissipative structures. I. Theoretical lines of convergence. In: GE Stelmach & J Requin (Eds.) *Tutorials in Motor Behavior*, pp. 3-45, Amsterdam: N-Holland Publ.
39. Feldman AG. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics.* 1966; 11:565-578.
40. Feldman AG. Once more on the equilibrium-point hypothesis (λ–model) for motor control. *J Mot Behav.* 1986; 18:17-54.

Citation: Latash ML. (2023). Mini-review: Biological Movements as Objects of Natural Science. *Brazilian Journal of Motor Behavior*, 17(6):288-293.
Editor-in-chief: Dr Fabio Augusto Barbieri - São Paulo State University (UNESP), Bauru, SP, Brazil.
Associate editors: Dr José Angelo Barela - São Paulo State University (UNESP), Rio Claro, SP, Brazil; Dr Natalia Madalena Rinaldi - Federal University of Espírito Santo (UFES), Vitória, ES, Brazil; Dr Renato de Moraes – University of São Paulo (USP), Ribeirão Preto, SP, Brazil.
Guest editor: Dr Vitor Leandro da Silva Profeta - University of Minas Gerais (UFMG), Belo Horizonte, MG, Brazil.

Funding: Nothing to report.
Competing interests: The authors have declared that no competing interests exist.
DOI: https://doi.org/10.20338/bjmb.v17i6.404