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Neurobiological tensegrity: The basis for understanding inter-individual variations in task performance?

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Abstract:

Bernstein's (1996) levels of movement organization includes tonus, the muscular-contraction level that primes individual movement systems for (re)organizing coordination patterns. The hypothesis advanced is that the tonus architecture is a multi-fractal tensegrity system, deeply reliant on haptic perception for regulating movement of an individual actor in a specific environment. Further arguments have been proposed that the tensegrity-haptic system is implied in all neurobiological perception and -action. In this position statement we consider whether the musculoskeletal system can be conceptualized as a neurobiological tensegrity system, supporting each individual in co-adapting to many varied contexts of dynamic performance. Evidence for this position, revealed in investigations of judgments of object properties, perceived during manual hefting, is based on each participant's tensegrity. The implication is that the background organizational state of every individual is unique, given that no neurobiological architecture (musculo-skeletal components) is identical. The unique tensegrity of every organism is intimately related to individual differences, channeling individualized adaptations to constraints (task, environment, organismic), which change over different timescales. This neurobiological property assists transitions from one stable state of coordination to another which is needed in skill adaptation during performance. We conclude by discussing how tensegrity changes over time according to skill acquisition and learning.

Keywords: Tensegrity; neurobiological systems; human movement; individual variations; perception-action coupling; skill acquisition

1. Introduction

Scientific interest in the nature of specific human-environment interactions has adopted different approaches and relied on varied theorical frameworks to understand how individuals regulate their behaviours (An, 2012; Luu et al., 2004; Warren, 2006). A key applied scientific aim is to unravel generalized laws to explain phenomena and gradually enrich human experiences and conditions. However, despite tendencies for behavioral analyses to be typically based on group average data, this endeavor has paradoxically revealed that individual variation seems to be an important constant in understanding functionality (e.g., Davids, Bennett, & Newell, 2006; Newell & Corcos, 1993). Nonlinearity in motor learning and development has been identified as a key source of the confounding effects of averaging data of participants and trials over time (Davids, Button, & Bennett, 1999; Newell, Liu, & Mayer-Kress, 2001). Here, we suggest how an understanding of the structural basis of neurobiological systems may provide some insights on the origin of such functional variations in movement behaviour. Nikolai Bernstein's work on the levels of movement organization suggests tonus as the muscular-contraction level that supports individual movement systems for (re)organizing coordination patterns (Bernstein, 1996). This background level, supporting the other levels of movement organization, was later hypothesized to possess a multi-fractal tensegrity architecture, predicated on the most significant medium of haptic perception (Turvey & Fonseca, 2014). James Gibson (1966) implied the prevalence of 'dynamic touch' (a subsystem of haptic perceptual system) in everyday life activities, leading (Turvey et al., 1998) to argue that "the role of dynamic touch in the control of manipulatory activity may be both more continuous and fundamental than that of vision"(p35).

Whereas Bernstein (1996) first suggested the crucial role of a background level of tonus, for action, (Gibson, 1979)recognized its importance for perception, which Turvey and Fonseca (2014) drew upon to unveil its structure and function. They promoted tensegrity as the proper characterization of the medium for the haptic perceptual system, contrasting with the original conceptualization which was considered a structural-architectural concept. We took Turvey and Fonseca's (2014) view and conceptualized their process of constant structural modulation and reconfiguration as a basis to formally understand and interpret individual differences in movement organization. In this position statement we seek to make the case that tensegrity properties can provide a basis for interpreting inter-individual variation in task performance. Conceptualizing the musculoskeletal system as a neurobiological tensegrity system, supporting a clear relationship with the personal coupling of perception and action, provides a starting point to understand the relevance of individualized variation in regulating goal-directed interactions (Araújo, Davids, & Hristovski, 2006). We first review the nature of tensegrity concepts in neurobiological systems and their relation to human movement, before advancing suggestions how they can form the basis of individual differences in performance.

2. Tensegrity in neurobiological systems

2.1 Tensegrity structures

Fuller (1962) coined the term "tensegrity" to describe structures that maintain their integrity by global tension in neurobiological systems. An important challenge is to consider how tensegrity in neurobiological systems can contribute to understanding individual differences in organization of perception and action. Tensegrity in neurobiological systems is an overall structure (there are structures within structures) with a particular set of properties, and most importantly, is a structure of functional primacy (Turvey, 2007). Functionality supported by tensegrity structures is sustained by their key properties: pre-stress, energetic efficiency, non-linear behaviours and omnidirectional stability. Pre-stress refers to the ongoing intrinsic tension that facilitates adaptability to behavioral changes. Such changes are induced by stress acting anywhere in the tensegrity system, and behavioral adaptability is expressed by changes in the configuration of the tensegrity structure, which spontaneously favor energetic efficiency. When stressed, tensegrity structures become stronger due to non-linear stiffening behaviours, independent of orientation with respect to gravity, maintaining stability in the structure to support system function (Scarr, 2014). Tensegrity in neurobiological systems can be observed at multiple scales, from the molecular dimension (Liedl et al., 2010) to the whole human movement system (Turvey & Fonseca, 2014). Tensegrity is not simply a component of a neurobiological system: it is a constitutive property of such systems. Research on embryological development showed that cytoskeleton cells' tensegrity architecture, and the mechanical forces they exert on extracellular matrices, are crucial for tissue pattern formation (Ingber, 2006). At a higher scale of observation, the spine, a structure so fundamental to most neurobiological behaviors, has tensegrity as the basis of its functionality. Conventional models of the spine, based on Newtonian laws, cannot explain the resilience demonstrated when it is subjected to common loads, other than compression, such as when adults pick up a child, or its functional adaptability to different performance environments (e.g., land, sea, air) or the energetic efficiency it exhibits in every action (Levin, 2002).

The haptic system also relies on tensegrity properties to efficiently underpin movement organization and regulation. Like other sensory systems, to propagate information, it requires a medium that needs to be place- and direction-invariant. Connective tissue in a broader macroscopic sense provides this medium, offering the necessary continuity and invariant properties (Turvey & Fonseca, 2014). Mangalam et al. (2020) showed the involvement of the whole-body tensegrity structure in task performance requiring judgments of object length and heaviness. Participants holding six different experimental objects varying in torque produced, mass and moment of inertia, registered fractal displacement fluctuations in the center of pressure, which all contributed to perceptual judgment of length and heaviness. Also, the fractality in center of pressure displacement increased across trials, highlighting an increased contribution to the perceptual judgment in a body location relatively distal from the hand holding the object (Mangalam et al., 2020). The relationship of haptic perception and movement is highlighted by the correlation of diminished haptic perception with lower motor abilities of children with developmental disorders (Tseng et al., 2019) and patients with Parkinson's disease (Mori et al., 2019). Fractality and complexity in the body are interlinked and ground interdisciplinary approaches in human movement science (Delignières & Marmelat, 2012). Recently, Cabe (2019) expanded on the hypothesis of tensegrity being the basis of all active movement. He made the point that any kind of environmental exploration (looking, listening, tasting, smelling, etc.) involves active movement and, therefore, is bound to engage each individual's tensegrity network.

2.2 Human movement and tensegrity

Bernstein's work (1996) on coordination remains fundamental to understand how human movement systems solve the degrees of freedom problem. The "infinite" possibilities of combined multi-articular movements (i.e., the degrees of freedom of each joint offer a countless set of possibilities) are reduced by the continuous (re)organization of functional coordinative structures (synergies) that exhibit the necessary consistency and flexibility to meet changing task demands. To Bernstein, the level of tonus (i.e., muscle-contraction level) primes the system to manage the necessary (re)organization of coordination patterns in skill adaptation. Indeed, "the basement level of tone" (Turvey & Fonseca, 2014, p.143) supports the muscular-ligament-skeleton to (re)organize complex movements. In either case, the pre-stress property of tensegrity structures provides system stability and adaptability when under mechanical perturbations.

Tensegrity supports movement production in neurobiological systems by facilitating force transmission (and information), which have to be considered beyond conventional descriptions of muscular-skeleton systems. A whole-body background force transmission system has to include fascia and recognize its role in connecting all other elements. In addition to the well-established process of muscles transmitting force to tendons, myofascial force transmission is another available path to produce joint movement. The relation between sarcomeres and the endomysium (a part of the extracellular matrix) allows myofascia to transmit force that can be placed at intra, extra and inter muscular levels (see Huijing, 2003 for details), driving a more integrative approach to understand the net force responsible for movement (Huijing, 2003). Differences in force between the proximal and distal insertions of a muscle, as well as changes in muscle length, exerting force in tendons of other muscles that are kept constant, corroborate the existence of epimuscular myofascial pathways (Maas & Sandercock, 2010). At the intramuscular scale of analysis, myofascial force transmission to the tendon can occur longitudinally (fasciotendinous transmission) or to the epimysium that surrounds the muscle. Extramuscular force is transmitted between a muscle epimysium and extramuscular connective tissue (e.g., neurovascular tract) and intermuscular force transmission occurs between neighboring muscles through connective tissue linked to the muscle belly (Huijing, 2003; Maas & Sandercock, 2010). Due to the inherent complexity of such a global system, *in situ* studies (Huijing & Baan, 2001; Maas, Baan, & Huijing, 2001; Rijkelijkhuizen, Baan, De Haan, De Ruiter, & Huijing, 2005) have produced more compelling evidence than *in vivo* experiments (Oda et al., 2007; Yaman et al., 2009). However, continuity of the myofascial system and force transmission has been determined in trunk and limbs (Krause et al., 2016; Wilke & Krause, 2019). To express this continuity (Myers, 1997a, 1997b) proposed a topology of different lines in the body. Myofascial chains are anatomical continuities of muscle and fascia that Myers (1997a, b) named according to their depth, location and role in the human body: Deep Anterior Line (DAL), Superficial Back Line (SBL), Superficial Anterior Line (SAL), Lateral Line (LL), Spiral Line (SL), Back Functional Line (BFL), Front Functional Line (FFL) and four (deep/superficial and anterior/posterior) Arm Lines (AL). There is strong evidence of the existence of the SBL, BFL, FFL and moderate evidence for the SL and LL (Wilke et al., 2016).

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Future research is needed to consolidate this evidence, and to verify the existence of the remaining lines, building on work from other studies which have confirmed lateral force transmission (Huijing, Maas, & Baan, 2003; Huijing, van de Langenberg, Meesters, & Baan, 2007; Huijing, Yaman, Ozturk, & Yucesoy, 2011; Yucesoy, 2010). Nevertheless, evidence of restored structure functionality (e.g., shoulder and lumbar spine), through manipulation of fascia based on the concept of tensegrity (i.e., manipulation in a different location other than the affected structure), highlights network connectivity (Grieve et al., 2015; Kassolik et al., 2013). The same approach has been shown to reduce lower back pain (Casato et al., 2019) that in some cases is caused by diminished mechanical properties of fascia (Langevin et al., 2009, 2011). Fascia, specifically fascial disorders, is also linked to a myriad of pathological conditions such as fibromyalgia (Liptan, 2010), lymphedema, deficient thermoregulation, diabetes, and deficient muscle function (Stecco et al., 2016). Taken together, this body of evidence suggests a relation between a less efficient fascial network and loss of functionality in systems and structures, sometimes accompanied by pain.

It is most important to consider the relevance of individual differences and between-participant variations in studies of fascia structure, location and mechanical properties. For example, in the transition between biceps femoris and the sacrotuberous ligament, a part of Myers superficial back line, high inter-individual variation in force transmission (7-69%) was observed, depending on differences in the sacrotuberous ligament fixation to the ischial tuberosity (van Wingerden et al., 1993). The plantar fascia, also part of the superficial back line, presents heterogenous morphology, locations and mechanical properties between sexes (Shiotani et al., 2019). The transition between adductor longus and the contralateral rectus abdominis, a part of the front functional line, also reveals high variation in mechanical properties among tested organisms (Norton-Old et al., 2013). An experimental study conducted by Kirilova et.al. (2011) on the mechanical properties of human abdominal fascia, part of the superficial anterior line, showed, as a rule, variability among individuals in stress-strain curves and other parameters such as maximal stress, stretch ratio at maximal stress and maximal stretch at rupture (Kirilova et al., 2011). Therefore, mechanical linkages to support coordinative structures are based on a tensegrity architecture and naturally benefit from the set of properties associated with it, underpinned by individualized morphologic, structural and functional differences.

2.3 Tensegrity and the basis for individualized Perception-Action

Tensegrity enables perception by priming and facilitating force transmission for individual interactions with the environment. From an ecological dynamics perspective, coupling perception and action, at the level of the performer-environment system (Araújo et al., 2006), tensegrity has to play a role in regulating goal-directed actions in specific performance environments. It has a significant role in synergy formation during adaptive behaviour. This can be evidenced by space travel data from long term exploratory journeys revealing how healthy individuals subjected to altered haptic perception exhibit poorer motor performance in skilled manual tasks. In microgravity (i.e., near zero gravity) conditions, there is less pressure and load on the body. These changing gravitational effects, in turn, reduce the contribution of haptic perception, with visible detriments in regulating actions such as aiming movements, tracking, grasping and complex movements. In microgravity, with practice, astronauts make adjustments to movements that reduce error, but adaption is never completed (Ross, 2008). In ecological dynamicsexplanations of movement organisation, synergies express the cooperation among component interactions to achieve an intended task-goal, retaining a context-dependent and structure-function relation (Profeta & Turvey, 2018). Ecological dynamics also implies a reciprocity and continuity of perception and action, with tensegrity architecture supporting self-organized coordination tendencies through both processes. Synergies are patterned (re)organizations of system components that, if necessary, can participate in other adapted coordination patterns with the same or different functions (Turvey, 2007).

Tensegrity is essential to movement in neurobiological systems, because it provides structural stability that enables the system to exhibit tendencies for degeneracy and metastability, hallmarks of adaptive behaviour. Degeneracy in neurobiological systems is a property indicating that the same output function can be achieved by structural variations in motor behaviour (Seifert et al., 2016). Degeneracy (like tensegrity) is present at every scale of biological organization, including: (i) the molecular level of genetic composition (Edelman & Gally, 2001), (ii) muscular-skeletal functioning (Dickinson et al., 2000), (iii) neural-network activation (Kelso, 2012), and (iv), complex, multi-articular actions (Seifert et al., 2014). For example, longitudinal data on infants' brain activity responding to looming-danger showed an intra-trial dynamic (re)organization of connectivity patterns consistent with degeneracy (van der Weel et al., 2019). The investigation focused on group differences between infants aged between 5-6 months and 12-13 months. Data presented revealed individual differences in looming-related visual evoked-potential responses and brain activity at the dipole visual cortex midline (van der Weel et al., 2019). In complex motor skills such as ice climbing, when compared to novices, experts show a more efficient performer-environment coupling (i.e., adaptive behaviour) that is predicated on a higher degree of degeneracy based on participants' perception of climbing affordances (Seifert et al., 2014). Evidence for this idea was provided by Hong and Newell (2006). They asked novices to learn a new coordination task on a ski simulator, expressing successful performance either by in-phase or anti-phase coupling between angular motion of the simulator and the learners' center of mass (COM) in the horizontal plane. Data revealed that, while maintaining performer-environment coupling, learners used different joint movement relations (i.e., exploiting system degeneracy) to achieve successful performance outcomes. Hong and Newell (2006) concluded that the role of freezing and freeing proposed by Bernstein (1996) on movement coordination is predicated not only in the intertwined relations between task, individual and environmental constraints, but also in inter-individual variations of search strategy in the perceptual-motor workspace (Hong & Newell, 2006).

Another important neurobiological property, metastability, may emerge when a system is placed under a set of specific task constraints, requiring it to perform under the influence of more than one system attractors, or in the present case, performance solutions (Kelso, 2012). A metastable state allows a neurobiological system to exploit degeneracy as the situation unfolds, which is common in dynamic complex environments. Metastability was earlier reported in an investigation of performance in a rhythmic bimanual coordination task (Jeka & Kelso, 1995), and has also been observed in more complex movement tasks (Davids & Araújo, 2010). Hristovski et al. (2006) showed that boxers performing a heavy bag punching task exploited inherent system degeneracy at a specific distance determined by the ratio of the distance to the target and the arm length of the participants. However, at shorter and longer distances, only one performance solution (attractor) emerged (Hristovski et al., 2006). In another sport task, cricket batting, task constraints manipulation also helped identify a metastable region of movement coordination tendencies. Manipulating ball bouncing location to correspond to four different regions when facing cricket bowling, movement timing and performance outcomes of batters were analyzed. Evidence revealed stable movement patterns in three regions and also one metastable region where highly diverse movement solutions emerged in batters (coordinating front foot and back foot hitting actions without directive instructions) to enhance performance functionality (Pinder et al., 2012).

The emergent actions of the individuals (boxers and batters) in these examples from sport performance are context-dependent and mediated by interactions with their intentionality (Araújo, Hristovski, Seifert, Carvalho, & Davids, 2017). The (re)organization of actions is based on the continuous coupling of perception and action provided by structures that exhibit tensegrity properties. Emergent movement solutions in metastable regions of performance are not identical for all performers, nor are they infinite (Rein et al., 2010). Thus, the number of simultaneous attractors and transitions between actions may be constrained by the structures responsible for perception-action. When performing the same complex task, skilled athletes exhibit metastability, which contrasts with performance of less skilled athletes. This observation indicates that metastability results from continuous perceptual motor adaptations that can be trained and developed with practice (Komar et al., 2014, 2015). Nevertheless, even skilled athletes show inter-individual variability in metastability regions in complex motor tasks (Rein et al., 2010).

3. Tensegrity and individual differences in performance

For tensegrity to provide a basis for understanding variations in individual-environment interactions, two concepts must be reconciled: homogeneity and individuality. The broader conceptualization of the neuro-muscular-fascial-skeleton system, as a multifractal tensegrity structure, provides homogeneity (i.e., a uniform structure and composition throughout). A medium with physical properties that are both place invariant and direction invariant (isotropic) (Turvey & Fonseca, 2014).This perspective has indicated that a tensegrity structure is dynamically sustained by properties of pre-stress, energetic efficiency, nonlinear stiffening behaviour and omnidirectional stability (i.e., maintains functional properties independently of gravity direction). Neurobiological individuality remains within the scope of a larger ongoing debate between philosophers and biologists. The question of what constitutes 'individuality' is still the subject of reflection (Pradeu, 2016), as well as how individuality should be conceptualized to address different behavioral questions (Love, 2015). Some conceptualizations of biological individuality are restricted to the performer, but here we focus on those that conceive individual behavior as inseparable from the environmental performance circumstances (Smith-Ferguson & Beekman, 2019). As mentioned, tensegrity is mostly a functional concept (Turvey, 2007), but structure and function are complementary (Kelso & Engstrom, 2006), in that the structure of initial conditions (with specific reference to organismic constraints) informs functional behaviors. The most basic form of structure variation is anatomical. Anatomical variation in the human movement system has been reported in: (i) muscles from head and neck (Harry et al., 1997), (ii) upper (Soubhagya et al., 2008) and lower limbs (Willan et al., 1990) and pelvis (Matejčík, 2010), (iii) the skeleton (Yoshioka et al., 1987), nerves (Adkison et al., 1991) and fascia (C. Stecco et al., 2013). Fascia has been classified according to its depth in the human body. Superficial fascia is a thin loose connective tissue that often separates anatomical structures, while deep fascia is dense connective tissue (C. Stecco et al., 2008). Guimberteau (2001, 2010) established the connection between the different layers with an impressive video analysis of a gliding system, a space filled with a vascularized collagen network that connects superficial and deep fascia. This network connects deeper and superficial tissue, allowing them to function differently and having a high proteoglycan content that behaves like a gel. This neurobiological property can only be observed in live or fresh tissue, and is, therefore, beyond the anatomical analysis usually performed in cadavers (Guimberteau, 2001; Guimberteau, Delage, McGrouther, & Wong, 2010).

With regards to inter-individual variations in movement performance, the whole-body tissue network that senses deformation and connects multiple layers of different structures has a chaotic cell arrangement, replete with non-linear behaviors. Therefore, the biophysics of behavior analysis needs to be grounded on methods different from those applied in engineering. To that intent, Muller (1996) explored the dynamics of a planar four-bar linkages system, suited to classify the complexity of biological movement. Although the human body has more complex structures than a four-bar linkages system, it was possible to capture changes in the bars' length in relation to the global geometry of the structure. The dynamics of the model (Muller, 1996) resonates with the aforementioned synergetic properties and tensegrity structures functioning, including: i) non-linear relations between structure shape and kinematic transmission parameters to obtain the most energetically-efficient mechanical behavior; and ii), the same mechanical properties available under different structure morphologies (Levin, de Solórzano, & Scarr, 2017). In sum, these properties *"permits a decoupling between morphologic diversity and function"* (Levin et al, 2017, p. 670), but paradoxically also allows the expression of individuality of the performer in the relation with the dynamical constraints of a particular performance environment. Considering the uniqueness of the myofascial system, based on tensegrity properties that supports the emergence of individual synergetic behaviors, it can be argued that the kinematics of a complex global movement form the observable expression of individuality within a specific context. Individuality in contextualised patterning of movements when interacting with the environment has been observed in gait (Nixon et al., 1999), running (Yam et al., 2004), playing musical instruments Clique ou toque aqui para introduzir texto.(Albrecht et al., 2014; Slater, 2020) and sport movements (Horst et al., 2020).

In goal-directed movement an individual's decisions emerge from the interaction of constraints (individual, task and environmental) and is grounded on the perception-action coupling process (Araújo et al., 2006). The individual's tensegrity network will be at the core of perception and action and "structure individuality", in terms of how it is expressed in a dynamic performance environment. This idea is key in an ecological dynamics perspective of skill learning (Davids, Araújo, Shuttleworth, & Button, 2003), suggesting that each individual performer needs to explore relevant system degrees of freedom (organismic and environmental) to discover which information variables are suitable to achieve a task solution. The relation between system interconnectivity and dexterity of action has been previously hypothesized (Harrison & Stergiou, 2015), however, future research needs to ascertain whether, with familiarity and experience, the individual's tensegrity network evolves to satisfy emerging task constraints. The individualized and global nature of the network guides future research to investigating a context-dependent framework and, whether focused on groups or individuals, towards more functional (Woody, 2015) rather than mechanistic (Fagan, 2015) scientific explanations. As the individual performer becomes attuned to task-relevant sources of information, task solutions emerge, constrained by an increasingly efficient tensegrity system. Interestingly, skilled athletes often present similar fitness levels to less skilled athletes (Chaabène et al., n.d.; Schaal et al., 2013) Contrary to a linear generalization, faster sprinters are not those with higher joint angular velocity or those applying greater amounts of force onto the supporting ground (Morin et al., 2011), but those who move faster over a certain distance. However, the skilled individual is able to exploit the perceptual-motor degrees of freedom to achieve multiple solutions to the same task goal, exploiting system degeneracy congruent with a "fine-tuned" tensegrity network supporting perception-action. In this process of skill learning, the tensegrity system does its “job”, explaining individual performance differences, based on its structural uniqueness.

4. Conclusion

In this position statement, we considered how the structure-function relationship in movement (re)organization in motor learning supports individual variations in skill development and performance. We considered whether the whole-body tensegrity system has a crucial role in establishing perception-action relations and needs to be considered for understanding the emergence of individual self-regulating trajectories in performance and development of learners over time. The tensegrity system, and the set of properties it encapsulates (pre-stress, energetic efficiency, nonlinear stiffening behaviour and gravity omnidirectionality), is an important medium for haptic perception (Turvey & Fonseca, 2014), being engaged in all exploratory actions (Cabe, 2019). It is also a fundamental part of force transmission that supports joint movements through a continuous and homogeneous distribution of myofascial tissue (Maas & Sandercock, 2010). Functionally adaptive behaviors emerge due to the tensegrity network’s capacity for degeneracy and the fluid transition among multiple system states or organization (meta-stability), which promote exploration, discovery and exploitation of different movement solutions. Such a structure exists in all individuals (Muller, 1996), but it is also unique for each individual, and this uniqueness shapes functionality in performer-environment systems. Further research is needed to discover more information on the novel concept of neurobiological tensegrity systems, not only on its properties, but also on discovering its trainability and exploitation for human learning, performance and skill development across the life course.

Declarations of interest
None

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