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This document is the Accepted Version [AM]

Citation:

SEIFERT, Ludovic, KOMAR, John, ARAUJO, Duarte and DAVIDS, Keith (2016).
Neurobiological degeneracy : a key property for functional adaptations of perception
and action to constraints. *Neuroscience & Biobehavioral Reviews*, 69, 159-165.
[Article]

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Pre-publication version: **NEUROSCIENCE & BIOBEHAVIORAL REVIEWS:**

<http://dx.doi.org/10.1016/j.neubiorev.2016.08.006> 0149-7634

Neurobiological degeneracy: A key property for functional adaptations of perception and action to constraints

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Abstract

A crucial aspect of understanding human behavior relates to the integration of perception and action sub-systems in coordinated and controlled movement during goal-directed activity. We aim to present how the neurobiological system property of *degeneracy* (i.e., many coordinative structures to achieve one function) can help understanding of the functional adaptations of perception and action to interacting constraints on performance. Since most research investigating degeneracy has been conducted in neuroanatomy, genetics and theoretical neurobiology, here we clarify how degeneracy is exhibited in perceptual-motor systems. Using an ecological dynamics framework, we highlight how degeneracy underpins the functional role of movement coordination variability in performance of multi-articular tasks. Following that, we discuss how degenerate neurobiological systems are able to exploit system stability and flexibility in their movement coordination. Third, we show how better coupling of information and movement could lead individuals to explore functionally degenerate behaviors. Last, we explore how degeneracy can support pluri-potentiality (i.e., one coordinative structure for many functions) as a way toward innovation or refinement in performance.

Key words: neurobiology, perceptual-motor systems, variability, adaptability, degeneracy, ecological dynamics.

1. Introduction

One crucial question to understand in explanations of human behavior relates to how movements are coordinated with the environment during goal-directed activity. This review emphasizes the role of *ecological dynamics* as a significant theoretical framework for analyzing behavioral adaptations to surrounding constraints based on using processes of perception and action. Ecological dynamics is a multi-dimensional framework shaped by multiple relevant disciplines which have been integrated to explain coordination and control processes in human movement systems during performance of complex multi-articular tasks (Araújo et al., 2013, 2006; Davids et al., 2015, 2012; Seifert et al., 2013a). Theoretical influences are provided by key concepts from ecological psychology (Gibson, 1979), nonlinear dynamical system theory (Haken, 1983; Kelso, 1995), and a complex systems approach in neurobiology (Edelman and Gally, 2001; Price and Friston, 2002; Tononi et al., 1998; Whitacre, 2010). In ecological psychology the continuous regulation of human behavior is predicated on the role of information that guides the behaviors of the individual–environment system (Gibson, 1979). The use of information is based on the perception of affordances which can solicit and constrain behaviors in a specific performance environment (Gibson, 1979; Withagen et al., 2012). The ecological approach has been enriched with the integration of tools and concepts from nonlinear dynamics to explain how information is related to the dynamics (including those of tasks and individuals) in a performance environment. Dynamical systems theorizing on human behavior (Kelso, 1995) addresses the emergence of coordination tendencies that exist between and within components and levels of complex neurobiological systems such as in human perception and action sub-systems. Ecological dynamics emphasizes the performer–environment system as the appropriate scale of analysis to explain behavior, based on several key assumptions that we discuss next.

The ecological dynamics framework advocates that coordination and control processes

in human behavior systems emanate from an emergent and intertwined relationship between the specific intentions, perceptions and actions of each individual, which continuously constrains the relationship between movement pattern stability and flexibility in each performer (Araújo et al., 2013; Davids et al., 2012, 2008; Seifert and Davids, 2012; Seifert et al., 2014a). Key theoretical issues arise from the study of the relationship *between coordination pattern flexibility (i.e., functional variability to adapt to a set of constraints) and stability (i.e., robustness of motor functions undergoing internal and external disturbances) under interacting performance constraints* (e.g., task, environment and personal) (Newell, 1986; Seifert et al., 2013a; Warren, 2006). Skilled performers are able to individually and functionally adapt their motor coordination patterns during performance, exhibiting degenerate behaviors. Degeneracy signifies that an individual can vary motor behaviors (structurally) without compromising function (Edelman and Gally, 2001; Mason, 2010; Price and Friston, 2002), providing evidence for the adaptive and functional role of coordination pattern variability in order to satisfy interacting constraints (Komar et al., 2015; Ludovic Seifert et al., 2014a; Seifert et al., 2013a, 2011).

Another important assumption for the ecological dynamics approach is that increasing expertise leads to a more functional *individual-environment relationship based on perception and action*. This development of expertise leads to enhanced capacity for skilled performers to utilize *affordances* compared to novices (Davids and Araújo, 2010a; Davids et al., 2015; Fajen et al., 2009; Withagen et al., 2012). This is because experts are more capable of exploiting information about environmental and task-related constraints to functionally (re)organize and regulate multiple motor system degrees of freedom to achieve consistent performance outcomes. According to the insights of James Gibson (1979), who defined *affordances* as opportunities for action offered by the environment, experts are more attuned to information for performance regulation than novices, supporting higher levels of task

achievement. Experts rely on a range of perceptual variables that specify relevant properties of a performance environment for achieving a task goal (Davids and Araújo, 2010a; Fajen et al., 2009; Richardson et al., 2008). This tighter information-movement coupling leads experts to exhibit degenerate behaviors, providing them with the flexibility to achieve the same performance outcomes with different coordination patterns. Research in ecological dynamics has demonstrated that degeneracy in complex perception-action systems provides the neurobiological basis for diversity of actions required to negotiate information-rich and dynamic environments for task goal attainment (Chow et al., 2009; Hristovski et al., 2006a; Seifert et al., 2014c).

More than ensuring stability against perturbations, and adaptations to dynamic environments, it is suggested that the degenerate architecture of neurobiological systems can help them exhibit *adaptability*, *creativity*, *innovation* and *evolvability*. This idea supports the hypothesis that degeneracy can support *pluri-potentiality* in complex systems (i.e. one structure can perform many functions) (Mason, 2010; Noppeney et al., 2004; Price and Friston, 2002; Whitacre, 2010). In particular, it is highlighted how some structures that are slightly mobilized under one set of constraints may potentially become much more mobilized under another set of constraints (Komar et al., 2015; Seifert et al., 2014b). The key property of *pluri-potentiality* invites a re-think of skill acquisition and transfer processes. For instance, it is advocated that the need to develop expertise by manipulating key constraints to support the exploration and emergence of adaptive patterns of coordination at a perceptual motor level is preferable to seeking to develop a common ‘ideal’ pattern of coordination, based on a putative expert model (Araújo and Davids, 2011; Davids and Araújo, 2010b; Seifert et al., 2013a).

Most research investigating degeneracy in neurobiological systems has been conducted in disciplines of cognitive anatomy, genetics and theoretical neurobiology, and has

mainly been concerned with the neural level of system architecture consider brain and behavior, perception and action together to highlight how degeneracy can help us to understand the functional and adaptive role of movement coordination variability in performance of complex multi-articular tasks in human behavior. To achieve that goal, our review is composed of four sections. The first section discusses the concept of degeneracy in comparison to that of redundancy, historically employed to explain human motor control. We also provide a definition of degeneracy from pioneer research in cognitive anatomy, genetic and theoretical neurobiology. The next three sections describe empirical support regarding the key ideas on degeneracy developed within the ecological dynamics framework.

2. Degeneracy supports stability and flexibility in neurobiological systems

Recent publications have highlighted the functional role of movement coordination variability, advocating an important role for the property of redundancy (Ranganathan and Newell, 2013; Wu and Latash, 2014). Redundancy has been defined as « *multiple ways to execute a movement to achieve the same task goal; this redundancy being present at several different levels in the system: multiple trajectories to reach the same external location in space, multiple joint configurations to produce the same end-effector location, multiple muscle activations to produce the same joint configuration* » (p. 65) (Ranganathan and Newell, 2013). This approach to movement coordination variability took roots in the initial problem posed by Bernstein (1967) about the multiple mechanical degrees of freedom, due to the great number of limbs, joints and muscles, that neurobiological motor systems have to organize. The number of degrees of freedom available in neurobiological motor systems is greater than the dimension of their workspace, the latter corresponding to the region of space within which a perceptual-motor system can move. Bernstein (1967) considered redundancy to be present when more than one motor signal can lead to the same trajectory of a given

motor system and defined motor coordination as « *the process of mastering redundant degrees of freedom of the moving organ, in other words its conversion to a controllable system* » (p. 127). For Latash (2012), the problem has been formulated incorrectly, « *there is no problem of motor redundancy; there is bliss of motor abundance* » (p. 1). Indeed, Gelfand and Latash (1998) and Latash (2012) suggested a principle of *abundance*, which considers the apparently redundant degrees of freedom as useful and even vital for many aspects, such as dealing with secondary tasks and unexpected perturbations. In the same ways, other researchers in cognitive anatomy (Friston and Price, 2003; Noppeney et al., 2004; Price and Friston, 2002), and genetics and theoretical neurobiology (Edelman and Gally, 2001; Sporns and Edelman, 1993; Tononi et al., 1999; Whitacre and Bender, 2010; Whitacre, 2010), have suggested that the concept of degeneracy is more appropriate than redundancy in analyses of functional behaviors in neurobiological systems. The concept of redundancy seems more suitable for studying performance of machines and engineering systems (Davids and Glazier, 2010; Latash, 2012; Newell et al., 2005; Tononi et al., 1999). In particular, Tononi et al., (1999) argued that « *redundancy refers to duplication or repetition of elements within electronic or mechanical components to provide alternative functional channels in case of failure* » (p. 3257), supporting the idea that redundancy provides a basis for great robustness in neurobiological systems. In other words, redundant systems reflect the presence of isomorphic and iso-functional components whereas degenerate systems are iso-functional but heteromorphic (Mason, 2010; Tononi et al., 1999). This latter property could be defined as « *the ability of elements that are structurally different to perform the same function or yield the same output* » (p. 13763) (Edelman and Gally, 2001). Therefore, for redundancy to occur, there must be the opportunity for redundant use of multiple structural configurations of elements, leading Friston and Price (2003) to argue that « *degeneracy is necessary for redundancy* » (p. 152). Finally, Mason (2010) proposed four avenues for degeneracy that

advance understanding of how neurobiological systems functionally adapt their behaviors to exhibit consistent outcomes in dynamic contexts. First, « *redundancy can create the opportunity for degeneracy to arise as the function of the original structure is maintained by one copy, while any other copy is free to diverge functionally* » (p. 282) (Mason, 2010). For example, in cognitive anatomy, if two neurons exhibit the same selective responses to a stimulus, this would correspond to redundancy, because the response of one could be predicted from the other (Friston and Price, 2003). Second, « *degeneracy can occur through parcellation, when an initial structure is subdivided into smaller units that can still perform the initial function and can also be functionally redeployed* » (p. 282) (Mason, 2010). Third, degeneracy may emerge through the assembly of a coordinative structure or synergy (Riley et al., 2012) composed of relevant system components for a specific function. This means that, whether a synergetic structure is able to perform an initial function independently, another one is available for modification (Mason, 2010), supporting *interchangeability* of different structures. For instance, in cognitive anatomy, lesions in the brain can appear to have little negative effect within familiar contexts which provides insights on the useful backup neural synergies which emerge (Friston and Price, 2003). Finally, degeneracy may exist when two or more independent structures converge upon the same function (Mason, 2010).

Therefore, as proposed by Newell et al.(2005), rather than being seen as a problem for prescriptive control, the many degrees of freedom can be seen as a wonderful resource, providing a degenerate (i.e., multi-structure) platform for the emergence and adaptation of behaviors in a dynamic complex neurobiological system. Like redundancy, degeneracy provides a high level of robustness in neurobiological systems, also enhancing *evolvability* in the sense that various synergies can achieve similar functions under certain conditions, but yet can perform distinct functions under other conditions (Whitacre, 2011, 2010; Riley et al., 2012). The presence of degeneracy in a neurobiological system increases its complexity and

robustness against perturbation and underlies its *pluri-potentiality*, a property that ensures an organism's functional ongoing engagement with the dynamic environment. Pluri-potentiality corresponds to a surplus of structures to deal with future performance situations, which means that some slightly mobilized synergies may potentially become much more mobilized in the future (Mason, 2010). In cognitive anatomy, this idea means that the same brain region can partake in multiple cognitive functions (Noppeney et al., 2004; Tononi et al., 1999). Degeneracy ensures robustness of function (i.e., stability) and supports pluri-potentiality in ensuring *evolvability* or *creativity* (Friston and Price, 2003; Noppeney et al., 2004). A key difference concerns is that degeneracy involves 'many synergetic structures to one function', while pluri-potentiality refers to a 'one synergetic structure to many functions' relationship (Mason, 2010).

3. Degeneracy supports stability and flexibility in perception-action systems

As highlighted previously, most of the literature on degeneracy and pluri-potentiality relates to cognitive anatomy and theoretical neurobiology in human behavior. However, recent studies have extended understanding of the role of degeneracy in *perception-action systems* in humans (Komar et al., 2015; Newell et al., 2005; Pinder et al., 2012; Rein et al., 2010; Seifert et al., 2014b, 2014c). Ecological dynamics advocates that there is an emergent and intertwined relationship between the specific intentions, perceptions and actions of each individual, which continuously constrains the relationship between *coordination pattern stability and flexibility* in each performer (Araújo et al., 2006; Araújo et al., 2013, Davids et al., 2012, 2008; Seifert and Davids, 2012; Seifert et al., 2014a). Here we emphasize the key theoretical issues that arise in studying the relationship *between movement pattern flexibility and stability under interacting performance constraints* (task, environment and personal) (Newell, 1986; Seifert et al., 2013a), to highlight how performers might individually and

functionally adapt their motor coordination patterns during performance. Both *stability* (i.e., persistent behaviors) and *flexibility* (i.e., variable behaviors) (Davids et al., 2003; van Emmerik and van Wegen, 2000; Warren, 2006) are essential to skilled performance under many different constraints, because it reflects adaptability. On the one hand, behavior is characterized by stable and reproducible movement patterns and transitions between them. These patterns are stable in the sense that functional forms of movement are consistent over time, resistant to perturbations and reproducible in that a similar pattern may emerge under different task and environmental constraints. On the other hand, movement behaviors are not stereotyped and rigid but flexible and adaptive. Although movement coordination patterns can reveal regularities and similarities within their structural components, an individual is not fixed into a rigidly stable solution, but can adapt movement coordination patterns in a functional way, as a function of system degeneracy. Adaptive behaviors, in which system degeneracy is exploited, signify that the perceptual motor system is stable when needed and flexible when relevant. In fact, although human movement systems naturally tend to seek relatively stable states for reasons of energy efficiency and economy (Hoyt and Taylor, 1981; Sparrow and Newell, 1998; Sparrow, 1983), *stability* and *flexibility* are not opposites on a continuum. Notably, *flexibility* is not a loss of *stability* but, conversely, is a sign of *adaptability* (i.e., a perceptual and motor adaption to interacting constraints), in order to facilitate (structural or not) changes in coordination patterns, at the same time, maintaining functional performance (van Emmerik and van Wegen, 2000; Warren, 2006). A crucial question is to understand which part(s) of behavior is(are) changed when a performer adapts to interacting constraints. Hong and Newell (2006) emphasized that individuals adapt high-order parameters of behavior (for example relative phase, a variable that describes coordination between limbs), by displaying locally different patterns of joint coordination, as similar global performance outcomes are achieved. In particular, in a ski-simulator task, Hong

and Newell, (2006) showed that participants can use both in-phase and anti-phase patterns of coordination between knee angular motions to reach the same performance outcomes (i.e., achieving the same coupling between the center of mass and the ski platform). Similarly, in cricket batting, skilled batters were able to functionally use forward (48% of time) and backward (52% of time) strokes to achieve task goals under similar constraints, i.e. when a bowler delivered the ball to a region of 6.5-7.5 m away from the stumps (Pinder et al., 2012). These data demonstrated how individuals exploited inherent system degeneracy, present in all neurobiological systems, to functionally achieve the task goal. In the same vein, Seifert et al. (2014b) manipulated task constraints for individuals swimming 200-m freestyle by constraining the glide duration (e.g., implementing a freely-chosen condition vs. maximal and minimal glide condition). They showed that swimmers were able to increase their leg beat-kicking (e.g., using ten beat kicks) to functionally adapt their behaviors when required to increase the glide phase with their arms. Findings revealed how swimmers were able to use inherent system degeneracy to overcome an atypical constraint on their stable movement patterns in order to satisfy the imposed task requirement.

4. The relationship between affordance utilization and motor system degeneracy

Another important concern of ecological dynamics is that the information that guides behaviors of complex neurobiological systems, is utilized through the role of *affordances* as a key relational property of the performer-environment system (Gibson, 1979). Affordances are particular properties of a performance environment, which are perceived in 'animal-relevant' terms (i.e., what they offer, invite or demand of an organism in terms of actions; Withagen et al., 2012). The concept of affordances provides a powerful way of understanding how processes of perception and action function in complex adaptive systems, since "*within the theory of affordances, perception is an invitation to act, and action is an essential component*

of perception" (Gibson, 1979, p46). Moreover, research has demonstrated that degeneracy in complex perceptual-motor systems provides the neurobiological basis for the diversity of actions required to negotiate information-rich, dynamic environments towards a task goal, as well as providing a huge evolutionary fitness advantage. Affordances are defined by the complementary relations between an individual and an environment. Affordances are action opportunities for an individual (Gibson, 1979), more recently interpreted as invitations to act (Withagen et al., 2012), which are predicated on knowledge *of* a performance environment (rather than knowledge *about*) (Araújo and Davids, 2011; Gibson, 1979). This type of knowledge highlights the importance of adopting a person-environment scale of analysis in an ecological dynamics rationale. Thus affordances are both objective and subjective to each performer (or neither, if one does not wish to get conceptually stuck into the classical divide between the organism and the environment), since they are ecological properties of the environment picked up relative to an individual (Scarantino, 2003; Turvey and Shaw, 1999). Affordances are specified within a unique frame of reference for each individual performer, whether learner or expert, adult or child, because they are specific to an actor's own action capabilities. Descriptions of the state of the environment are 'frame dependent' because affordances are perceived relative to relevant properties of an individual (i.e., they are body-scaled, including the scale of key body dimensions, e.g., height, limb sizes). The relationship between the physical properties of the environment and the individuals' action capabilities can be captured in the perception of an affordance (Withagen et al., 2012). In climbing, affordances refer to "climbing opportunities" (Boschker et al., 2002), i.e., environmental properties that invite reach-ability, grasp-ability and climb-ability of holds on a vertical surface. In rock climbing, Boschker et al., (2002) demonstrated how experts recalled more information specifying the *functional* properties of a climbing wall (e.g., surface textures, orientations and shapes: knowledge *of* a performance environment), neglecting to perceive its

structural features (e.g., properties like color and size: knowledge *about* a performance environment). Conversely, novices were not able to recall such functional properties of the wall to support their actions and they tended to report almost exclusively the structural (less functional) features of the holds (Boschker et al., 2002). For instance, if a rock climber grasps a surface hold because of its large size, instead of its shape or its orientation, he/she may be using the wrong structural feature (e.g., hold size instead of hold shape or hold orientation) to decide which hold to grasp and how to grasp it (Seifert et al., 2013b). An affordance in rock-climbing specifies what a hold is and, therefore, what a hold means, unified in one perceiving-acting process. Perceiving opportunities for specific actions requires perceptual attunement to and calibration to relevant informational variables, meaning that individuals need to pick up a range of perceptual variables from different system modalities (haptic, kinesthesia, auditory, visual) that specify a relevant property of a performance environment (Fajen et al., 2009; Jacobs and Michaels, 2007). The term 'relevant' signifies functionality, as this property enables an individual performer to achieve a specific task goal. An important characteristic of experts is their perceptual attunement to relevant informational variables, revealing that they are better at perceiving task-specific affordances than beginners. This is because experts are more capable of exploiting information about environmental and task-related constraints to functionally (re)organize the multiple degrees of freedom of the body to achieve consistent performance outcomes. However, degeneracy can also be observed in novices, especially when they explore different coordination solutions to achieve a task goal. For instance, when novice boxers were requested to punch a heavy-bag, they explored a varied range of striking patterns involving 'uppercuts', 'hooks' and 'jabs' at a critical value of 0.6-scaled distance to target (Hristovski et al., 2009, 2006b). Hristovski et al., (2006a) suggested that the perception of a 'strike-ability' affordance (i.e., the perception of the scaled distance to a target) might explain the emergence and exploration of various boxing striking patterns, exploiting

degeneracy of perceptual motor systems. These findings are important in understanding the acquisition of complex multi-articular skills since they exemplified how placing a performer's perceptual and action systems under certain task and environmental constraints enhanced their exploratory behaviors. This finding is also supported by data on performance during a climbing task in a challenging environment (i.e., a frozen waterfall), highlighting how high perceptual attunement and calibration to environmental properties supported skilled climbing performance (Seifert et al., 2014c). Investigating skill-based differences in this climbing task, Seifert et al. (2014c) suggested that existing holes in the icefall provided affordances to regulate performance in expert climbers, leading to emergence of degenerate behaviors. In particular, experts used a wider range of upper and lower limb coordination patterns, resulting in the emergence of different types of action (e.g., ice tools swinging, kicking and hooking actions). In contrast, beginners displayed lower levels of degeneracy in perception and actions systems, due to a lack of perceptual attunement and calibration to environmental properties (e.g., shape, steepness, temperature, thickness and ice density) and leading them to produce similar and repetitive type of actions and a narrower range of coordination patterns, to anchor ice tools (Seifert et al., 2014c). In sum, individuals can perceive affordances in order to satisfy a set of constraints by varying their motor behaviors (structurally) without compromising function, providing evidence for inherent neurobiological system degeneracy (i.e., through the emergence of adaptive and functional movement pattern variability).

5. Degeneracy supports creativity, innovation or evolvability in perception-action systems

More than simply ensuring stability against perturbations and adaptations to a dynamical performance environment, the degenerate architecture of neurobiological systems can exhibit *creativity*, *innovation* or *evolvability*, leading to the hypothesis that degeneracy

(i.e., many structures to one function) can support pluri-potentiality (i.e., one structure to many functions) (Mason, 2010; Noppeney et al., 2004; Price and Friston, 2002; Whitacre, 2010). For instance, Rein et al. (2010) analyzed full-body kinematics during performance of a basketball hook shoot and highlighted that the skilled players could exploit two to six different patterns of coordination to shoot at the same target from different distances, exploiting the presence of system degeneracy. Although high inter-individual behavioral variability was also observed through the different throwing distances (between two and nine meters), the investigators showed that two players were able to slightly adapt their elbow–shoulder and knee–hip coordination pattern and to maintain low fluctuations in shooting scores (Rein et al., 2010). For these players, pluri-potentiality emphasized the robustness of the synergy that they assembled for shooting from many target distances. Similarly, our research has highlighted how, in an aquatic locomotion task (i.e., breaststroke swimming), swimmers can adapt the same arm-leg coordination pattern at different swimming speeds, by generating higher levels of velocity and acceleration with their limbs during propulsion (Komar et al., 2015, 2014). In particular, pluri-potentiality (i.e., one structure to many functions; Mason, 2014; Noppeney et al., 2004) was exhibited through a stable kinematic pattern of arm-leg coordination between high and low speed conditions during propulsion, which generated higher velocity and acceleration in high speed conditions (Komar et al., 2014). The adaptations reside mainly in the time spent gliding with the lower and upper limbs fully extended (meaning that coordination between arms and legs did not change during this phase because the limbs remained immobile in a streamlined position). However, the consequences of a higher level of acceleration during leg propulsion led to greater distances covered during the glide phase (Komar et al., 2014). Finally, it was shown that by using stable arm-leg coordination patterns during propulsion and flexible glide durations, expert swimmers could modulate the velocity of their center of mass, and thus vary swimming

speeds. This perceptual motor adaptation to aquatic resistances was only observed in expert swimmers. Indeed, recreational swimmers demonstrated changes in arm-leg coordination between high and low speed conditions during propulsion, which prevented effectiveness (e.g. velocity achieved and distance covered by the center of mass) of their coordination pattern (Komar et al., 2014). Further investigations of arm-leg coordination in breaststroke swimming have emphasized that degeneracy can also support pluri-potentiality as it reflects greater flexibility of a coordination pattern i.e., higher range of functions, such as coping with a larger range of aquatic resistance in order to swim faster (Komar et al., 2015) and to optimize the glide by minimizing active drag (Seifert et al., 2014b). These findings illustrated how, some structures slightly mobilized under one set of constraints may potentially become much more mobilized under another set of constraints (Mason, 2014, 2010). For instance, when swimmers are required to swim at a fixed swimming speed (paced by an operator), but maintaining or decreasing an extensive glide duration, with the body fully extended, they not only change the kinematic pattern of coordination between arms and legs (that reflects degeneracy), but they also minimize active drag by using a more streamlined body position (e.g., flattening trunk inclination; using higher arm extension during leg propulsion; employing better synchronization between the beginning of the leg propulsion phase and the end of arm recovery). These functional adaptations demonstrate how individuals (particularly skilled performers) are able to increase the flexibility of their coordination patterns, which in return exhibits structural evolvability toward greater functional creativity and innovation.

6. Conclusion

In this review paper we have discussed key concepts in ecological dynamics that demonstrate the inherent degeneracy in neurobiological systems such as humans. Exploiting inherent degeneracy, especially in perception and action systems, allows skilled individuals to

achieve the same performance outcomes by re-organizing system degrees of freedom (different structural components) into functionally useful task-oriented synergies. We have discussed how skilled individuals maintain a subtle functional balance between stability and variability in movement patterns exemplified in different sport performance environments such as climbing, swimming, boxing, and cricket batting. At the heart of this adaptive process is the regulation of action by information, captured by affordance utilization in skilled interactions with performance environments.

7. Highlights

- Degeneracy supports stability and flexibility in perception-action systems.
- Affordance utilization can explain degenerate behavior.
- Degeneracy supports creativity and evolvability in neurobiological systems.

Acknowledgment

This project received the support of the High Network of Research CPER-LMN “Logistics, Mobility and Numeric” 2016-2019.

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