Neuroscience and Biobehavioral Reviews 69 (2016) 159–165

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

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

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ARTICLE INFO

Article history:
Received 8 June 2016
Received in revised form 20 July 2016
Accepted 5 August 2016
Available online 6 August 2016

Keywords:
Neurobiology
Perceptual-motor systems
Variability
Adaptability
Degeneracy
Ecological dynamics

ABSTRACT

A crucial aspect of understanding human behavior relates to how perception and action sub-systems are integrated during coordinated and controlled movement in goal-directed activity. Here we discuss how a neurobiological system property, *degeneracy* (i.e., many coordinative structures to achieve one function), can help us understand how skilled individuals functionally adapt perception and action to interacting constraints during 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 perceptual-motor functions) as a way toward innovation or refinement in performance.

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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 con-

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

tinuous regulation of human behavior is predicated on the role of information that guides behaviors of the individual–environment system (Gibson, 1979). The use of information is founded on 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 related to tasks and individuals) of 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 constrain 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; Seifert et al., 2014a, 2013a, 2011). The concept of degeneracy originated in the sub-disciplines of cognitive anatomy, genetic and theoretical neurobiology, highlighting how neurobiological systems (like humans) not only demonstrate degeneracy at the neural level, but also at the level of perception and action in behavior regulation. It must be clarified that degeneracy has nothing to do with *degeneration*. Mason et al. (2015) has suggested introducing a hyphen to distinguish *degeneration*, (the undesirable degradation of a system) from degeneracy (a completely separate technical term denoting many structures to one function).

An important hypothesis for examination within the ecological dynamics approach is whether increasing expertise leads to a more functional relationship between an *individual and a performance environment, predicated on perception and action*. The development of expertise leads to the 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, continuously, 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 (e.g., see Chow et al., 2009; Hristovski et al., 2006a; Seifert et al., 2014c).

These studies have shown that, more than simply ensuring stability against perturbations and adaptations to dynamic performance environments, the degenerate architecture of neurobiological systems can help individuals exhibit *adaptability*, *creativity, innovation* and *evolvability*. This idea supports the hypothesis that degeneracy can support exploitation of *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 even more mobilized under another set of constraints (Komar et al., 2015; Seifert et al., 2014b). This key property of *pluri-potentiality* invites a re-think of skill acquisition and transfer processes (notably the *specificity* of skill transfer; Seifert et al., 2016). Skill transfer emerges from the influence of prior experiences under a particular set of interacting constraints on performance under a different set of conditions, compared to those where the skills were originally acquired. Thus, *specificity* of transfer can emerge under practice task constraints where existing performance disposition or tendencies of an individual cooperate with the dynamics of a new task to be learned, facilitating emergence of successful performance behaviors (Seifert et al., 2016). Therefore, it is hypothesized that the need to develop expertise by manipulating key task constraints to support exploration and emergence of adaptive patterns of coordination at a perceptual motor level is preferable (because it would favor skill transfer) 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). In other words, a key hypothesis from that perspective is that a higher skill level reflects the capacity to achieve the same performance with many different movement coordination patterns (reflecting in some ways the ability of an individual to adapt and to transfer his/her skills), rather than a single specific pattern.

Most previous research investigating degeneracy in neurobiological systems has been conducted in sub-disciplines of cognitive anatomy, genetics and theoretical neurobiology. This work has mainly been concerned with the neural level of system architecture considering brain and behavior, perception and action together, highlighting how degeneracy can help us to understand the functional and adaptive role of movement coordination variability in performance of complex multi-articular tasks. Our review of neurobiological degeneracy and its implications 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. The next three sections describe empirical support regarding key ideas on degeneracy developed within the ecological dynamics framework. It will become clear that system degeneracy is a cornerstone of coordination of actions in experts with respect to performance environments. In particular, we describe how degeneracy supports stability and flexibility in perception-action systems. Then we show how degeneracy between neurobiological systems (i.e. between individuals) captures individual actualization of affordances through variable coordination patterns. Last, we highlight how degeneracy unlocks the power of pluri-potentiality (i.e. creativity, innovation or evolv-