Neurobiological degeneracy: Supporting stability, flexibility and pluripotentiality in complex motor skill

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ABSTRACT

This paper investigated neurobiological degeneracy of the motor system that emerged as a function of levels of environmental constraint. Fourteen participants performed a breaststroke-swimming task that required them to develop a specific biomechanically expert pattern and in turn provide the basis for a suitable task vehicle to study the functional role of movement variability. Inter-limb coordination was defined based on the computation of continuous relative phase between elbow and knee oscillators. Unsupervised cluster analysis on arm–leg coordination revealed the existence of different patterns of coordination when participants achieved the same task goal under different levels of environmental constraints (i.e. different amounts of forward resistances). In addition, clusters differed in terms of higher order derivatives (e.g., joint angular velocity, joint amplitude), suggesting an effective role for degeneracy in learning by allowing the exploration of the key relationships between motor organization and interacting constraints. There is evidence to suggest that neurobiological degeneracy supports the potential for motor re-organization to enhance motor learning.

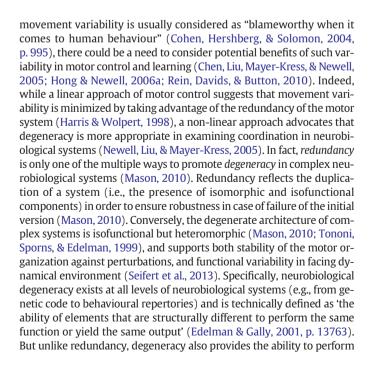© 2014 Elsevier B.V. All rights reserved.

1. Introduction

From an ecological dynamical perspective (see Seifert, Button, & Davids, 2013 for a review), human beings can be considered as complex dissipative structures with numerous degrees of freedom in a dynamical environment, leading to the emergence of alternative conceptualizations of processes related to perception, cognition, action and decision-making (Williams, Davids, & Williams, 1999). The key emphasis from an ecological dynamical perspective alludes that the emergence of goal-directed behaviour is a consequence of self-organization through the continuous performer–environment interaction (Kelso & Engström, 2006).

Recently, the study of supra-coordinative task (i.e., a task for which the goal is not to produce a specific coordination pattern, Faugloire, Bardy, & Stoffregen, 2009) provides a suitable platform to reconsider the functional role of movement pattern variability (e.g., Hong & Newell, 2006a; Rein, Button, Davids, & Summers, 2010). While

movement variability is usually considered as "blameworthy when it comes to human behaviour" (Cohen, Hershberg, & Solomon, 2004, p. 995), there could be a need to consider potential benefits of such variability in motor control and learning (Chen, Liu, Mayer-Kress, & Newell, 2005; Hong & Newell, 2006a; Rein, Davids, & Button, 2010). Indeed, while a linear approach of motor control suggests that movement variability is minimized by taking advantage of the redundancy of the motor system (Harris & Wolpert, 1998), a non-linear approach advocates that degeneracy is more appropriate in examining coordination in neurobiological systems (Newell, Liu, & Mayer-Kress, 2005). In fact, *redundancy* is only one of the multiple ways to promote *degeneracy* in complex neurobiological systems (Mason, 2010). Redundancy reflects the duplication of a system (i.e., the presence of isomorphic and isofunctional components) in order to ensure robustness in case of failure of the initial version (Mason, 2010). Conversely, the degenerate architecture of complex systems is isofunctional but heteromorphic (Mason, 2010; Tononi, Sporns, & Edelman, 1999), and supports both stability of the motor organization against perturbations, and functional variability in facing dynamical environment (Seifert et al., 2013). Specifically, neurobiological degeneracy exists at all levels of neurobiological systems (e.g., from genetic code to behavioural repertoires) and is technically defined as 'the ability of elements that are structurally different to perform the same function or yield the same output' (Edelman & Gally, 2001, p. 13763). But unlike redundancy, degeneracy also provides the ability to perform

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different functions under different conditions (Mason, 2010; Whitacre, 2010). Critically, degenerate elements may share the same function, but unlike redundant elements, they do not share the same over-all structure.

For instance, in a ski-simulator task, Hong and Newell (2006b) showed how different participants were able to use different inter-limb coordination patterns to reach the same performance outcomes. When knee motion relations were examined, both in-phase and anti-phase coordination patterns were exhibited by the participants with the presence of an effective coupling between the center of mass and the ski platform (i.e., the same effective outcome). From Hong and Newell (2006b), it was concluded that locally, different joint organizations could occur although similar global function was achieved. Similarly, Rein, Button, Davids, and Summers (2010) analyzed the full-body kinematics of basketball hook shoot and reported high inter-individual differences in elbow–shoulder and knee–hip coordination during the execution of the shots at the same target distance (with distances tested varying from 2 to 9 m). In addition, Rein, Button, Davids, and Summers (2010) also highlighted multiple pathways of adaptation with reference to different throwing distances. When performance of cricket batting was investigated, Pinder, Davids, and Renshaw (2012) demonstrated how individuals exploited system degeneracy to functionally adapt stable movement pattern solutions to satisfy changing task constraints (e.g., forward or backward movements). These results provided strong empirical support for the emergence of a functional degenerate behavior in multi-articular movements. Indeed, it appears that when several movement patterns are available, learners can individually exploit the inherent degeneracy present in neurobiological systems to achieve the task goal.

In addition to ensure stability against perturbations and adaptation to dynamical environment, it is suggested that the degenerate architecture of neurobiological systems plays a central role in adaptive innovation of complex system (Hristovski, Davids, & Araújo, 2006; Whitacre, 2010). It creates the potential for variations and encourages "pluripotentiality" (Mason, 2010, p. 281). Specifically, pluripotentiality refers to the potential involvement or removal of biomechanical degrees of freedom to increase stability or flexibility of the system. More precisely, there are opportunities for the human movement system to acquire two or more coordination patterns, sometimes partially sharing same elements (e.g., partially sharing same joints), to accomplish a task. For instance in catching a ball, one can essentially coordinate his shoulder, elbow and wrist to reach the ball, but could also move and coordinate his entire body while additionally involving his hip, knee and ankle to realize the task. This partial use of possible joints offers the possibility to always involve additional degrees of freedom into the overall coordinative structure to ensure task realization. In other words, degeneracy may allow a surplus of degrees of freedom necessary for later exaptation (Mason, 2010). Degeneracy therefore plays an important role in learning, providing the basis for the diversity of actions required to negotiate information-rich environment, as well as providing huge evolutionary fitness advantage (Seifert et al., 2013). Importantly, the acquired coordination is a product of self-organization and the instances of exploration (i.e., variability during learning) are an inherent part of the learning process (Newell, 1991; Sporns & Edelman, 1993). Chow, Davids, Button, and Koh (2008), in a soccer kicking study, further observed that there were actually no common pathways of change in coordination pattern during learning, suggesting that directional changes in degrees of freedom were dependent on task relevant intrinsic dynamics. Inevitably in the process of skill acquisition, the pathway to organize joints was different across participants, suggesting the functional role of degeneracy during learning.

One framework that could yield insights into the functional role of system degeneracy is Newell's model of learning with three stages of learning (coordination, control and skill, Newell, 1985). Early in learning (i.e. between coordination and control stage) novices are challenged to seek for a functional assembling of the body parts regarding task and environmental conditions. Once reached the control stage, performers

are able to perform with consistency in changing performance environment. Later during learning, skill stage is observed when performers are able to use reactive forces from their muscular–skeletal system or from the environment to efficiently achieve the task. Specifically, for learners who are navigating between coordination and control stage of learning, there is a need to progressively become more attuned to the consequences of different combinations of key variables in impacting the task behaviour. Degeneracy may therefore support the explorative activity of learners involved in the transition between those two stages (see Chow et al., 2008).

Interestingly, swimming represents a supra-coordinative task, but it is assumed that a biomechanically effective pattern of coordination between elbow and knee oscillations seems to be adopted by expert performers compared to novices (Seifert et al., 2011). For example, experts were able to start a swimming cycle with arm–leg coordination in anti-phase followed by an in-phase mode and then back to anti-phase mode through every cycle of movement (i.e., every 1–2 s). In aquatic activities where the environmental constraints play an important role (e.g., due to high density of water), the use of a biomechanically effective pattern becomes pertinent for effective performances (Seifert, Leblanc, Chollet, & Delignières, 2010). In addition, the level of environmental constraint (i.e., the amount of forward resistance swimmers have to overcome in order to move) is related to the swimming speed squared (see Toussaint & Truijens, 2005), therefore an increase in swimming speed leads to quadratic increase of environmental constraints. It is therefore unclear whether learners need to actively explore the perceptual-motor workspace when learning a specific biomechanical expert pattern during their transition between coordination and control stage of learning, or instead converge directly towards this biomechanical expert pattern.

This paper aims to investigate the role of neurobiological degeneracy in the acquisition of coordination in a task where the perceptual-motor workspace is highly constrained and the existence of a biomechanically effective expert pattern is assumed. More precisely, the objectives were to: i) determine if there is inherent degeneracy for a swimming task; ii) determine how the level of constraints can limit the expression of degeneracy; and iii) explore how degeneracy can support a functional role for movement variability. We then hypothesized that even if the desired outcome of learning is the acquisition of a single biomechanically effective pattern, active exploration of the workspace can be facilitated by the inherent neurobiological degeneracy. In addition, it is predicted that participants who are seeking for a functional coordination (i.e., between coordination and control stage of learning, Newell, 1985) may exhibit different patterns of coordination reflecting explorative behaviours. Whereas stability and accuracy are usually the features of the movement to define an optimal learning (Tallet, Kostrubiec, & Zanone, 2008), the findings from this study may highlight the critical role played by neurobiological degeneracy and especially pluripotentiality property as a way of acquiring skill flexibility during the learning process.

2. Method

2.1. Participants

Fourteen breaststroke swimmers with an equivalent level of expertise and representing a range of recreational level swimmers (i.e., assessed by two experienced swimming instructors and motor control specialists as navigating between coordination and control stage of learning based on Newell's model of learning) were recruited for this study. Expertise level was expressed as a percentage of the current world record (W.R.) based on their best performance for 50-m breaststroke. Six women and eight men (18.9 ± 1.0 years, 62.2 ± 8.5 kg, 1.72 ± 0.63 m height; time measured on the day of the test for 25 m: 22.1 ± 2.5 s; best performance for 50 m: 38.89 ± 4.41 s that represents 63.70 ± 7.25%W.R.) were recruited for this study. The protocol,