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THE ROLE OF MOTOR VARIABILITY IN MOTOR CONTROL AND LEARNING DEPENDS ON THE NATURE OF THE TASK AND THE INDIVIDUAL'S CAPABILITIES

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ABSTRACT

Recent studies have found that motor variability is actively regulated as an exploration tool to promote learning in reward and error-based tasks. Based on this functional role of variability, several researches have manipulated motor variability by practicing in order to maximize learning processes. However, the effectiveness of such variable practice as a tool to improve motor performance has shown several controversial results. The present work reviews how the interaction between the features of individuals with different motor capabilities (i.e. experience and brain disorders) and task constraints modulates the relation between motor variability and motor control and learning. Examining how the process of skill learning can be improved by the variability modulation according to individuals' is not only of theoretical interest, but may also have several practical implications in motor learning and neuro-rehabilitation.

Key words: motor learning, variable practice, constant practice, individuals' capabilities, motor variability, task constraint, neurological disorders

EL ROL DE LA VARIABILIDAD MOTORA EN EL CONTROL Y APRENDIZAJE MOTOR DEPENDE DE LAS CARACTERÍSTICAS DE LA TAREA Y LAS CAPACIDADES INDIVIDUALES

RESUMEN

Estudios recientes han demostrado que la variabilidad motora es activamente regulada como herramienta de exploración con objeto de incrementar el rendimiento motor tanto en tareas de aprendizaje basadas en la aplicación de recompensas como en la percepción del error. Basándose en este rol funcional de la variabilidad, varios investigadores han manipulado la variabilidad motora al practicar para maximizar los procesos de aprendizaje motor. Sin embargo, la efectividad de la práctica variable como herramienta para la mejora de la ejecución motora, ha mostrado resultados contradictorios en la literatura científica. El presente trabajo revisa cómo la interacción entre las características de individuos con diferentes capacidades motrices (i.e. experiencia y alteraciones neurológicas) y las características de las tareas modulan la relación entre la variabilidad motora, el control y el aprendizaje motor. El estudio de cómo los procesos de aprendizaje motor pueden ser mejorados mediante la manipulación de la carga de variabilidad al practicar no tiene sólo un interés teórico, sino que puede tener implicaciones prácticas en relación al aprendizaje motor o la neuro-rehabilitación.

Palabras clave: aprendizaje motor, variabilidad en la práctica, práctica constante, características individuales, variabilidad motora, constreñimiento de la tarea

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INTRODUCTION

Motor variability as a functional feature of the motor system and its relationship with performance and the ability to adapt.

Motor variability has been traditionally interpreted as an error of the system. This "error" is mainly related to the mechanisms involved in the muscle contractions needed to run a motor program, introducing noise (variability) and movement inaccuracy. That is why motor variability has been used to classify skill level (Churchland, Afshar, & Shenoy, 2006; Harris & Wolpert, 1998; Osborne, Lisberger, & Bialek, 2005; Reina, Sarabia, Yanci, Garcia-Vaquero, & Campayo-Piernas, 2015; R. A. Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979; Shmuelof, Krakauer, & Mazzoni, 2012). However, in literature, it has also been underlined that human movement variations could provide useful information about the characteristics of individual's motor control and the capability to adapt (Barbado, Sabido, Vera-Garcia, Gusi, & Moreno, 2012; Caballero, Barbado, & Moreno, 2015; Manor et al., 2010; Wu, Miyamoto, Gonzalez Castro, Olveczky, & Smith, 2014). From this perspective, it is suggested that the central nervous system (CNS) regulates motor variability in order to ease the exploration of the large number of possible configurations offered by the many motor system degrees of freedom (DOF) that can lead to a desired solution (Barbado et al., 2012; Davids, Glazier, Araujo, & Bartlett, 2003; Wu et al., 2014).

This latter functional perspective of motor variability is not in opposition to the traditional role of variability in human movement control. There are two different interpretations of motor variability related to two variability dimensions: magnitude and structure (Caballero, Barbado, & Moreno, 2014; Stergiou, Harbourne, & Cavanaugh, 2006). In order to address the assessment of both dimensions, the use of different tools, such as linear and nonlinear tools, is required. Nevertheless, the choice of the most appropriate tools to assess motor variability remains controversial (Caballero et al., 2014; Goldberger, Peng, & Lipsitz, 2002; Stergiou & Decker, 2011). Nowadays, it is fully accepted that the assessment of both dimensions might help to identify the underlying process of human motor control in different tasks and in individuals with different capabilities (Goldberger et al., 2002; Stergiou & Decker, 2011).

Recent studies have evidenced the relationship between motor variability with performance and learning processes. Some researchers have found that higher magnitude of variability is related to a better performance (Bauer & Schöllhorn, 1997) and faster learning (Wu et al., 2014). Other works, in which the structure of variability has been analyzed, suggest that variability structures with higher degrees of irregularity and less auto-correlated are positively linked with better performance (Caballero, Barbado, Davids, &

Moreno, 2016; Caballero et al., 2015; Duarte & Sternad, 2008; Stins, Michielsen, Roerdink, & Beek, 2009), adaptation ability (Barbado et al., 2012; Manor et al., 2010; Zhou et al., 2013) and faster learning (Barbado, Caballero, Moreside, Vera-García, & Moreno, 2017). All these findings support that movement variability is a functional tool of the CNS because it helps individuals to adapt their behaviors to environmental changes (Davids, Bennett, & Newell, 2006; Davids et al., 2003; Renart & Machens, 2014; Riley & Turvey, 2002). As it was stated in the past decade by Davids et al. (2003)*"variability has a functional role in helping individuals adapt to ever-changing constraints imposed on them by environmental, anatomical and physiological changes due to disease, illness, injury and aging"* (p. 251). It may be noted that the functional role of motor variability is not an unmodifiable property of the human system; conversely, it may be actively regulated by the CNS to promote learning (Churchland et al., 2006; Mandelblat-Cerf, Paz, & Vaadia, 2009; Sober, Wohlgemuth, & Brainard, 2008). Recent works in songbirds have found that the neural circuits involved in motor variability promote learning by directing the exploration of motor output space (Andalman & Fee, 2009; Warren, Tumer, Charlesworth, & Brainard, 2011) confirming that variability seems to be regulated and indeed amplified in the nervous system to improve learning processes (Wu et al., 2014).

However, the relationship between variability and motor control remains controversial and it is not one-way, but it seems to depend on: i) the nature of the intrinsic dynamics of the system, and ii) the task constraints (Caballero et al., 2016), which determines the skill progress (Barbado et al., 2017). In this instance, we will focus on the intrinsic characteristics of the individual, like the skill level of the participant, its capabilities or even its intentions, and how it seems to have an effect on variability dynamics and its relation with the performance and the learning process (Borg & Laxaback, 2010; Van Orden, Holden, & Turvey, 2003; Washburn, Coey, Romero, Malone, & Richardson, 2015). Nevertheless, specific task constraints must also be taken into account due to the fact that individual characteristics are environmental dependent. For example, changes in task constraints might lead to an increase or a reduction in the number of motor configurations available, affecting the motor variability dynamics during performance (Caballero et al., 2016; Davids et al., 2003; Newell & Vaillancourt, 2001).

One example of the interconnection between intrinsic and extrinsic constraints, and its effect on the motor variability, would be the learning stages, which may depend on the experience of the learner or the novelty/difficulty of the task. Previous findings indicated the need for high-variability when exploration is required to learn a novel task, but low-variability improves performance when exploiting a viable solution (Woolley & Doupe, 2008; Wu et al., 2014).

In the present work, it is proposed to review how different motor capabilities of individuals and their interaction with task constraints can modulate the relation between motor variability and motor control and learning. Understanding this relationship is a significant step to be able to move forward and manipulate motor variability to improve performance and learning.

Variable practice as a useful tool to enhance learning processes.

As it has been mentioned above, motor variability has been associated with functional adaptive behaviors (Davids et al., 2006; Davids et al., 2003; Renart & Machens, 2014; Riley & Turvey, 2002) and higher learning rate (Barbado et al., 2017; Manor et al., 2010; Zhou et al., 2013). Therefore, it would be reasonable to think that an increased variability in the motor system could drive the emergence of exploratory behaviors, which involve a better ability to adapt and, as a result, it would promote faster learning rate. Years ago, this idea was suggested, under the schema theory R. A. Schmidt (1975), who proposed that variable practice facilitates the development of rules about motor behavior, acquiring a flexible schema, which is able to adapt to a continuously changing environment. Although the schema theory postulates that variable practice would be beneficial for all tasks, Gentile's model (1972) stipulated that close skills require consistency because fixation of movement is necessary (Eidson & Stadulis, 1991), suggesting that constant practice would lead to better results during learning. Thus, variable practice would not be appropriate to promote faster learning during tasks such as archery, in which the environment is highly predictable and the motor behavior can be planned (Lee, Magill, & Weeks, 1985; Shapiro, Schmidt, Kelso, & Clark, 1982; Van Rossum, 1990). In this kind of task, constant practice would allow to stabilize the motor pattern reducing motor “noise” caused by stochastic neuromuscular function (Churchland et al., 2006; Harris & Wolpert, 1998; Osborne et al., 2005; R. A. Schmidt et al., 1979; Shmuelof et al., 2012) and, thus, increase task performance. However, in a certain sense, the division of tasks in “open” or “closed” may be arbitrary. No environment is entirely predictable and, even in the most stable situations, no equal actions are possible because the motor behavior is produced by the nervous system, which is inherently noisy (Dhawale, Smith, & Olveczky, 2017; Faisal, Selen, & Wolpert, 2008; Renart & Machens, 2014; Stein, Gossen, & Jones, 2005). Based on this assumption, it is reasonable to think that variable practice could also be useful for learning closed skills, in which all the conditions are always (or seems to be) the same. Variability induced by practice would allow the individual to adjust their motor behavior to the changes caused by environment-individual interaction.

Findings from recent studies support that practicing under variable conditions in different close skills (i.e. tennis serve or hurdling) improve task performance in higher extent than constant practice (Hernandez-Davo, Urban, Sarabia, Juan-Recio, & Moreno, 2014; Menayo, Moreno, Fuentes, Reina, & Damas, 2012 ; Savelsbergh, Kamper, Rabius, De Koning, & Schöllhorn, 2010; Schollhorn, Beckmann, & Davids, 2010; Schöllhorn, Beckmann, Janssen, & Drepper, 2010). These results support the idea that variable practice challenges the apprentice with a variety of movements that cover a whole range of possible motor solutions for a specific task, which could be modulated by the learner, even when the task conditions apparently stay unchanged (Moreno & Ordoño, 2015). However, scientific literature has also shown opposite results that question the utility of variable practice for closed skill learning. Some studies have found that constant practice shows better (Edwards & Hodges, 2012; Shea, Lai, Wright, Immink, & Black, 2001; Zipp & Gentile, 2010) or similar results (Elfaqir, 1982; Johnson & McCabe, 1982; Pigott & Shapiro, 1984; Wrisberg & Mead, 1981, 1983) than variable practice in this type of skills.

These controversy results lead us to consider what the possible causes are. As it was mentioned in the previous section, the individual's characteristics and the task constraints may modulate the role of motor variability during learning. Therefore, it is reasonable to believe that they also affect the functionality of variable practice as a tool to optimize learning rate.

The benefits of the variable practice depends on the task constraints and individuals features.

In the acquisition and development of a skill, a learner passes through different levels of proficiency until becoming an expert. To achieve this aim, coaches and teachers do not apply a similar practice schedule during the different learning stages but, in fact, they do modify the training conditions, such as *practice load* according to learner's individualities. As previous authors have stated (Garcia-Herrero, Sabido, Barbado, Martinez, & Moreno, 2016; Moreno & Ordoño, 2015) motor variability is an unavoidable property of all biological systems which is not fully possible to eliminate. Thus, constant practice does not exist. Conversely, all kind of practice induces, more or less, motor variability according to the individuals' features. Therefore, the effectiveness of a practice schedule may probably be related to the amount of intrinsic motor variability that the practice induces on each individual rather than the practice features themselves. This reasoning would explain why some authors have found higher performance improvement in a novice after variable practice than a constant one (Douvis, 2005; Kerr & Booth, 1978; Wulf, 1991) while, as it has been showed above, other ones found opposite results (Garcia-Herrero et al., 2016). Owing this fact, *load of variability* should be one of the relevant aspects to be modulated to optimize learning processes. In fact, there are some evidences which suggest that variable and constant practices have a differential effect on learning, depending of the individuals' characteristics (Garcia-Herrero et al., 2016). However, to the best of our knowledge, there is limited evidence about studies analyzing the effects of the different *load of variability* (Moreno, Peláez, Urbán, & Reina, 2011).

Some studies have shown that, during the learning of accuracy manual tasks, adults benefited from variable practice while children did not (Lee et al., 1985; Shapiro et al., 1982). These results seem to be similar with those observed in a meta-analysis about the differential effect of contextual interference (randomized and blocked practice) on adult and child individuals (Brady, 2004). This meta-analysis showed that higher levels of variable practice condition (randomized) promotes higher learning rates in adults than blocked practice, but not in children. Authors like Wulf and Schmidt (1994) pointed out that random practice might produce an excessive variability response in child, hindering the development of a stable motor solution to achieve the task demands. Analogous findings have been observed comparing expert and novice with similar ages. Garcia-Herrero et al. (2016) showed that expert handball players only improved their overarm throwing accuracy under variable practice whilst novices displayed greater improvements practicing under constant conditions. These authors suggest that higher skilled individuals exploit their current knowledge rather than explore for a new motor solution, so it is necessary to enhance their motor variability in order to promote exploratory strategies (Barbado et al., 2017) which allows them to refine their motor behavior according to changes in external and/or internal constraints (Seifert, Button, & Davids, 2013). Conversely, a novice typically displays an inherent variability that facilitates the exploration for a more stable and efficient motor solutions (Barbado et al., 2017; Garcia-Herrero et al., 2016; Ranganathan & Newell, 2013). Thus, enhanced levels of variable practice would be counterproductive in less skilled individuals because it would induce excessive motor configurations according to the novice capabilities, delaying the choice of the most appropriate of them to accomplish the task requirements (Wulf & Schmidt, 1994). Based on these results, it should be necessary to apply an individualized load of variability in practice according to individual features. However, to the best of the authors knowledge, only one study has tested this hypothesis (Moreno et al., 2011). These authors applied different *load of variability* in practice in a novel throwing skill finding that intermediate levels of variability showed the best accuracy improvement, compared with higher and lower levels of practice variability. According to the results, we postulate that it could be an optimal amount of variability to optimize the learning process according to learner characteristics.

Multiple individuals' characteristics could modulate the efficiency of variable practice on motor learning. The learner's level in performing a skill may be influenced by different individuals' capabilities, not only the experience. For example, researchers have examined the effects of variable practice in individuals with intellectual impairments (Eidson & Stadulis, 1991), finding that variable practice may promote faster learning in transfer tasks with relatively simple environmental demands (i.e. closed skills). Nevertheless, in this study, constant practice produces greater performance improvement in tasks with more complex environmental demands (i.e. open skills). Although these findings initially seem to be opposite to previous results found in literature about the benefits of variable practice in open skills (Hernandez-Davo et al., 2014; Menayo et al., 2012 ; Savelsbergh et al., 2010; Schollhorn et al., 2010; Schöllhorn et al., 2010), they agree with the idea that when the learner exhibits large variability in the motor response (according to each individual's characteristics) it may be inappropriate to induce more motor variability.

Studies on individuals with spastic CP (i.e. impaired cerebral cortex) have suggested that the high levels of motor variability showed by these individuals, may hinder the learning during the acquisition of a new motor skill (Damiano, Stanley, Ohlrich, & Alter, 2017; Gofer-Levi, Silberg, Brezner, & Vakil, 2013). Due to abnormal muscle co-activations, some authors have suggested that a constant practice is necessary in order to learn a new skill, although a delayed improvement should be expected (Hung & Gordon, 2013). Furthermore, Gofer-Levi et al. (2013) state that individuals with CP tend to assimilate better the explicit components of the motor learning (i.e. planning process) through instructions and feedback while, presenting limitations in the learning of implicit components (i.e. execution process). Therefore, from a practical point of view, practitioners should gradually present the new skills and providing constant practice in order to enhance motor learning (Gofer-Levi et al., 2013).

The damage in specific brain structures, which govern movement control, is also expected to have a unique (and, thus, differential) influence on the role of movement variability in motor learning probably specific on the way that a task is learned. In this regard, circuits involving the basal ganglia seem to play a fundamental role during reward-based learning manipulating the amount of motor variability during practice to enhance performance (Ramayya, Misra, Baltuch, & Kahana, 2014; Wu et al., 2014). In this learning mechanism, subjects are required to explore in order to determine which actions will lead to success and those movements are reinforced. In this sense, motor variability can be considered an essential component of reinforcement learning, where the exploration necessary to gather knowledge must be balanced with exploitation of the knowledge that has been accrued (Kaelbling, Littman, & Moore, 1996; Sutton & Barto, 1998). Consequently, it would be expected if basal ganglia is damaged, the subjects' ability to manipulate their motor variability for functional purposes during reward-based learning would be hindered. Confirming this hypothesis, Pekny, Izawa, and Shadmehr (2015) found that, although adults with Parkinson disease initially showed similar levels of motor variability during a reward-modulated discrete task than their peers without neurological alterations, when the rewarded target region was modified, they displayed a limited ability to amplify their motor variability to explore the task space and achieve the reward. An interesting question arisen from Chu, Sternad, and Sanger (2013) was that children with impaired basal ganglia (dystonia) were able to move towards an optimal strategy to achieve a good functional variability (as well as their peers without neurological disorders did), during a manipulandum rotating task in which the learning was not based on reward mechanisms but in the perception of the error.

Error-based adaptation is another form of learning and probably the most extensively studied in literature. Error-based learning requires subjects to have access to the error arising from their action, and it is typically driven by predictable perturbations to a movement corrected on a trial-by-trial basis (Shadmehr, Huang, & Ahmed, 2016). Error-based adaptation need not be contingent on such exploration and, therefore, variability plays a different role in learning, even when a reduction of the motor variability is required to achieve good performance (Barbado et al., 2017; Wu et al., 2014). Error-based learning not only depends on exploration but individuals' ability to measure and predict the motor error. This type of learning has been related to cerebellar structures of the brain, which seem to play a central role in learning and timing of movements (Broersen et al., 2016). Disorders resulting from the impaired cerebellum (Friedreich Ataxia, CP) tend to cause abnormalities in the scaling of movements and in the coordination of limbs and trunk voluntary movements (Gagnon et al., 2014; Morton & Bastian, 2004). Furthermore, studies conducted with individuals with ataxia (i.e. damage located primarily in the cerebellum) have showen how these individuals presented poor performance and limited learning ability in manual visuomotor tasks (Shmuelof et al., 2012; Therrien, Wolpert, & Bastian, 2016). This indicates that impaired cerebellum impacts on individuals' sensory prediction-error-based learning, and impeding effective responses to a visuomotor disturbance, demonstrating a low sensitivity to error. Based on these results, it has been suggested that, in order to maximize motor learning in this population, the variability of the designed tasks should be reduced as much as possible. Based on the fact that reward-based learning allows learners to adjust their movement without relying on sensory prediction mechanisms, some studies have postulated that reinforcement learning might represent an alternative mechanism for motor learning in individuals with cerebellar damage (Izawa & Shadmehr, 2011). Conversely, as it seems to be supported by the differential findings observed in the Pekny et al. (2015) and Chu et al.'s (2013) studies mentioned above, error-based learning could be the best option for motor learning in individuals with basal ganglia disorders. However, the independency between CNS structures and, thus, learning mechanism, does not seem to be as clear. Therrien et al. (2016) found that cerebellar damage indirectly impairs reinforcement learning by the increased motor noise produced by the alteration in the cerebellum. These authors postulate that optimal reinforcement learning requires a balance between exploration variability and motor noise.

In summary, we have tried to show that the functional role of variability in motor learning depends on task constraints and relies on the individuals' intrinsic characteristics. In this instance, we have focused on the intrinsic characteristics of the individual, like the skill level of the participant and their capabilities. The analysis of motor variability can provide useful information to characterize motor performance and learning, but this relation has to be addressed in relation to the different motor capabilities of the individuals, either due to their performance level or due to alterations in voluntary movement control. Examining how the process of skill learning can be enhanced is not only of theoretical interest, but may also have practical implications in motor learning and neurorehabilitation (Shishov, Melzer, & Bar-Haim, 2017). Interventions in which variability is experimentally manipulated according to the individuals' characteristics remain a poorly explored area, especially in populations with diverse capabilities (Chu et al., 2013). Future research is needed to clarify the functionality of variable practice as a tool to optimize learning rate.

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