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Review

Repetition and variation in motor practice: A review of neural correlates

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ABSTRACT

Random practice results in more effective motor learning than either constant or blocked practice. Recent studies have investigated the effects of practice schedules at the neurophysiological level. This study aims to conduct a literature review of the following issues: (a) the differential involvement of premotor areas, the primary motor cortex, the dorsolateral prefrontal cortex and the posterior parietal cortex in different types of practice; (b) changes in the participation of these areas throughout practice; and (c) the degree of support that current neurophysiological findings offer to strengthen the behavioral proposition that distinct cognitive processes are generated by different practice schedules. Data from 10 studies that investigated associations between practice structures and neurobiological substrates were analyzed. The participation of the indicated areas was found to depend on practice structure and varied during the learning process. Greater cognitive engagement was associated with random practice. In conclusion, distinct neural processes are engendered by different practice conditions. The integration of behavioral and neurophysiological findings promotes a more comprehensive view of the phenomenon.

Contents

1. Introduction

The number of skills that are practiced during a session and the order in which the skills are performed interferes with the quality and quantity of information that is received, processed and generated by the learner (Gonçalves et al., 2007). Thus, different learning levels are expected when comparing different types of practice

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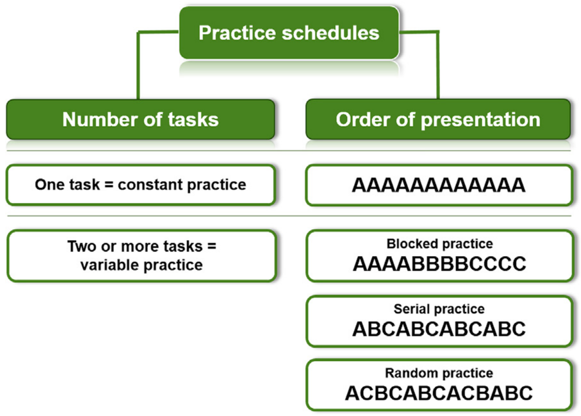

Fig. 1. Types of practice schedules in terms of number of tasks practiced and orders of skill presentation.

organization. There are two basic practice schedules: constant and variable (Fig. 1). Constant practice consists of learning only one skill during a practice session, while variable practice refers to learning two or more skills (Shea and Kohl, 1990).

The variability of practice hypothesis claims that variable practice is more effective at inducing schema development than is constant practice (Moxley, 1979). When a movement is executed, a learner strengthens his/her schemas, storing information about (a) the initial conditions, (b) the response specifications of the motor program, (c) the sensory consequences of the produced response, and (d) the effects of the movement on the environment (Schmidt, 1975). A greater variety of experience within a given movement class (e.g., an overhand volleyball serve) produces a stronger schema. Thus, variable practice leads to greater increases the transfer capability to a novel variation of the same movement class than does constant practice. However, this hypothesis does not distinguish which subtype of variable practice, such as random versus blocked practice, is the most effective. Conversely, previous studies on the contextual interference effect (Sekiya and Magill, 2000; Sekiya et al., 1996, 1994; Wulf and Lee, 1993) have assumed that learning is differentially affected by different variables of practice and have investigated which practice variables promote better learning.

Contextual interference is the effect on the learning produced by the order of skills changing across trials (Shea and Morgan, 1979). A non-systematic order of skills execution, as well as a non-consecutive execution of the same skill (A-C-B-C-A-B-A-B-C), is observed during random practice. Conversely, blocked practice is characterized by a systematic order of skill execution and the consecutive execution of all trials of a given skill before the execution of the block of another one (A-A-A-B-B-B-C-C-C). The high contextual interference that is associated with random practice and serial (A-B-C-A-B-C-A-B-C) practice promotes better learning than the low contextual interference that is associated with blocked practice (Magill and Hall, 1990; Sekiya et al., 1994).

High contextual interference promotes better learning because it requires greater cognitive effort during the execution of motor skills. Two cognitive hypotheses have been proposed to explain the contextual interference effect. The elaborative-processing hypothesis developed by Shea and Zimny (1983) proposes that random practice requires a higher level of intratask and intertask comparisons between trials, leading the learner to undergo further elaboration and distinction in memory than blocked practice (Fig. 2). More elaborate information processing results in more comprehensive and readily retrievable memory traces. The forgetting-reconstruction hypothesis, or action-plan reconstruction hypothesis, proposes that random practice promotes the forgetfulness of a previously constructed action plan because the learner has to perform a different task during the next trial. This process involving the forgetting and reconstruction of action plans strengthens the representation of these skills in memory (Lee and Magill, 1983) (Fig. 3). Conversely, during blocked practice, this process does not occur across repeated trials of the same task. Both the elaborative-processing and forgetting-reconstruction hypotheses support the notion that different levels of cognitive engagement are associated with different practice schedules during the learning process.

Beyond the traditional behavioral level of analysis, other levels of analysis can be used to investigate the effects of practice organization on motor learning. Neuroscience-based inquiries can extend the current level of knowledge regarding the processes involved in the acquisition of motor skills (Kantak and Winstein, 2012) and reveal existing correlations between the cognitive processes that are involved in motor control and the neural substrates that support these processes (Seidler, 2010).

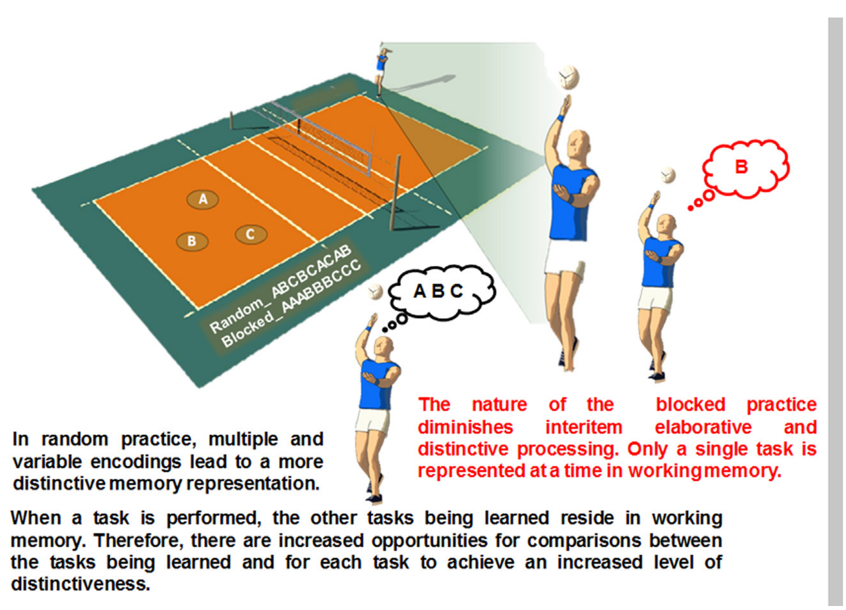

Fig. 2. Higher levels of distinction and elaboration are induced by random practice.

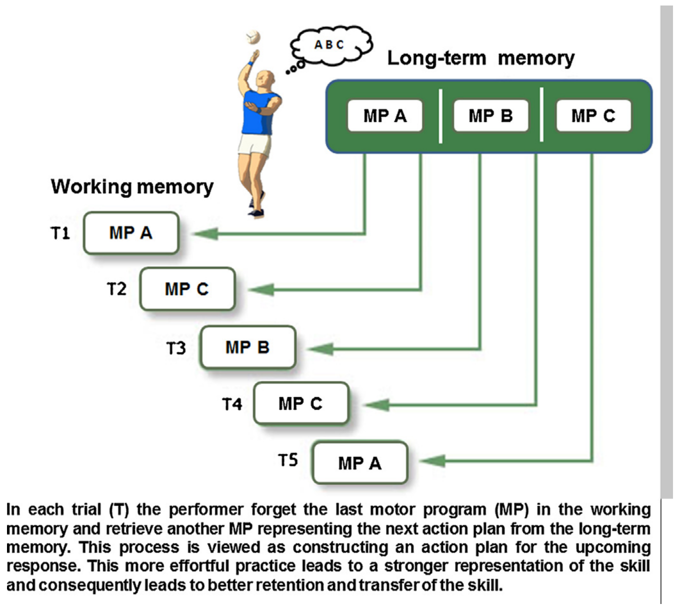

Fig. 3. Action plan reconstruction during every attempt in random practice.

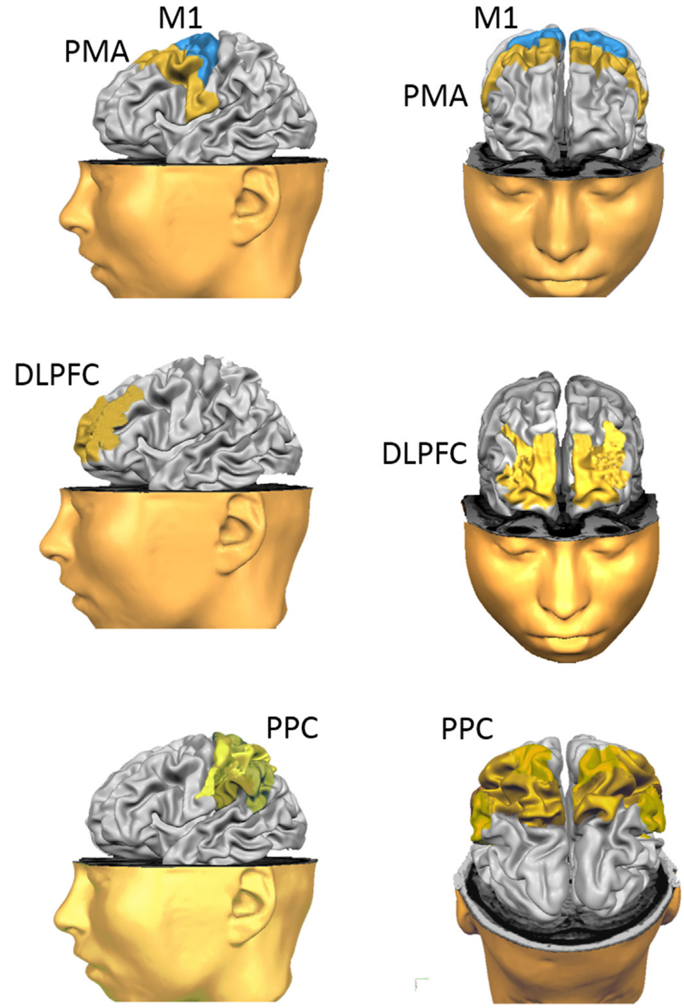

Fig. 4. (A) M1 and PMA (PMC and SMA) localization; (B) DLPFC; (C) PPC. (Image adapted from BrainVoyager Brain Tutor software).

Motor learning is associated with the recruitment of circuits involving regions of the frontal lobe, which is divided anatomically into three main areas: the prefrontal cortex, the primary motor area and the premotor areas (Miller, 2007). The primary motor area (M1) and premotor areas (PMA) make up the premotor cortex (PMC), and the supplementary motor area (SMA) is critical in the planning and execution of movement (Fig. 4A). The formation of motor representations requires a functional reorganization of these areas and of other subcortical areas throughout the process of practice, leading to greater involvement of the corticostriatal system than the cortico-cerebellar system at the end of practice (Doyon et al., 2003).

Theoretical propositions that integrate cortical areas related to cognition and motor control have been presented since the 2000s. Brain regions that were previously seen as disconnected in both a functional and anatomical sense have become perceived as being interconnected. The dorsolateral prefrontal cortex (DLPFC; Fig. 4B), a critical area for complex cognitive functioning, seems to contribute to motor performance (Diamond, 2000), as it has extensive interconnections with regions involved in motor functions, such as the PMC and the SMA (Dum and Strick, 1991). The DLPFC critically contributes to memory processing (Cohen and Robertson, 2011) and motor planning (Tanji and Hoshi, 2008), which are two important aspects of the study of practice organization. Moreover, the DLPFC is engaged in motor-memory consolidation (Muellbacher et al., 2002).

Another important cortical area involved in motor learning and control is the parietal cortex. The posterior parietal cortex (PPC; Fig. 4C), including both its inferior and superior regions, is associated with the functions of integration and scaling during planned movements (Cohen and Andersen, 2002) and participates in changing the neural representation of memory to contribute to motor consolidation (Shadmehr and Holcomb, 1997). Frontal-parietal networks, including the PPC, the DLPFC and the PMA, are involved in sequence learning (Ziemann et al., 1995).

The general roles of these cortical areas during motor learning are well known. However, the specific associations of these areas with different practice schedules have been a theme in several recent studies. The integration of this recent, scarce knowledge is important for obtaining the answers to the following pertinent questions: First, do the participation levels of the premotor, motor, dorsolateral and posterior parietal regions vary between different practice structures? Second, over the course of a single type of practice, do these levels change? Finally, do neurophysiological findings strengthen the behavioral proposition that different cognitive processes are generated by different practice schedules? The aim of this study was to conduct an integrative review of the literature that has investigated the effects of practice organization at the neurophysiological level to answer these questions.

2. Methods

The current integrative review consisted of several stages. The first stage focused on elaborating the investigative questions that need to be answered. Based on a set of inclusion and exclusion criteria, article selection was conducted during the second stage. Next, a description of the studies and results was constructed. Finally, the results were interpreted, and a final report was compiled (Mata et al., 2011; Whittemore and Knafl, 2005).

We focused on the following questions to guide this integrative review: Do the participation levels of the PMA (PMC and SMA), M1, DLPFC and PPC vary across different practice schedules? Throughout the practice process, does the involvement of the PMA, M1, DLPFC and PPC vary? What cognitive processes are employed during different practice schedules?

The following inclusion criteria were used: (a) articles investigating issues related to practice organization from a neuroscience perspective, (b) articles that included samples with healthy subjects, (c) articles that were published between January 2005 and August 2014, and (d) articles that were published in English. The publication period was defined from a previous analysis of the literature. Review articles, case studies, opinions and studies that did not provide detailed descriptions of the methods used were excluded.

Articles available in PubMed, ISI Web of Science and Scopus were evaluated. In the PubMed database, the following terms were used in an advanced search: "Motor Skills/physiology" [MeSH Terms] AND "Neural Pathways/physiology" [MeSH Terms]. A total of 198 articles were found. In the ISI Web of Science database, 7 articles were found using the search terms "Neural substrates" AND "Practice structure" AND "Cortex". In the Scopus database, 704 articles were found through quick search by using the terms "Motor Learning" AND "Neuroscience. The search parameters (MeSH Terms and keywords) for each database were defined based on a previous analysis. We adopted different parameters for each database because we found that the effectiveness of a given set of search terms varied between databases.

In total, 909 articles were found. To define the study sample, we read the titles and summaries of all of the articles. In uncertain cases, the full article was read. Applying the aforementioned inclusion and exclusion criteria, six articles were included in the study based on the agreement of the authors T. A. S. and G. M. L. After selecting the articles, T. A. S. and G. M. L. discussed the consistency of the data found within, and ultimately, each study was individually analyzed for final inclusion. The authors then conducted a reverse search from the references of the six included articles to identify additional potential articles for inclusion. Four articles were included from this reverse search, for a final sample of ten articles.

The main variables of study were findings correlating structures of practice and the activation of target cortical areas. Secondarily, the following additional characteristics of the studies were analyzed: (a) production characteristics (publication period, publication journal and researchers' countries of origin), (b) motor tasks used, (c) dependent measures used, (d) analysis techniques used, and (e) main behavioral and neurobiological findings.

Because the terminology used to describe different anatomical brain regions varied across studies (Courtney, 2004), we standardized the descriptions of the anatomical regions of interest (the PMA, M1, DLPFC and PPC) based on the analysis of gyri, sulci and/or activated circuits.

The terms "acquisition phase", "retention" and "transfer" were respectively used to describe the period of practice, the consolidation of the motor skill(s) practiced and the adaptability of the motor skill(s) practiced. Descriptive analyses of absolute frequency were used.

3. Results

All ten articles that comprised the sample were published between 2007 and 2013 in the following scientific journals: Nature Neuroscience (Kantak et al., 2010), Journal of Motor Behavior (Kantak et al., 2011; Lin et al., 2008, 2009), Journal of Neurophysiology (Wymbs and Grafton, 2009), Neuroimaging (Lin et al., 2011), Cerebral Cortex (Song et al., 2012; Tanaka et al., 2010), Journal of Cognitive Neuroscience (Cross et al., 2007) and Human Brain Mapping (Lin et al., 2013). All of the studies were conducted in the United States of America.

Regarding the types of practice evaluated in the articles, eight studies compared the effects of variable random and blocked practice (Cross et al., 2007; Lin et al., 2008, 2013, 2011, 2009; Song et al., 2012; Tanaka et al., 2010; Wymbs and Grafton, 2009), and two studies compared the effects of constant practice and variable random practice (Kantak et al., 2011, 2010). Five studies used keystroke sequence tasks (Cross et al., 2007; Lin et al., 2013, 2011; Song et al., 2012; Wymbs and Grafton, 2009), four studies used aiming tasks with two reverse movements of flexion and extension of the elbow (Kantak et al., 2010; Lin et al., 2008, 2009), and one study used a sequential aiming task (Tanaka et al., 2010). The samples in all of the studies were composed of young adults. Only four studies indicated that participants were naïve to the task (Kantak et al., 2010; Lin et al., 2008, 2009; Song et al., 2012). However, the simplicity of the tasks that were used in the other studies also suggested that the participants were naïve.

The four main measures used in the tasks were reaction time (Song et al., 2012; Wymbs and Grafton, 2009), movement time (Cross et al., 2007; Tanaka et al., 2010; Wymbs and Grafton, 2009), time of response (reaction time plus movement time) (Lin et al., 2011; Tanaka et al., 2010; Wymbs and Grafton, 2009), and root mean square error (Kantak et al., 2011, 2010; Lin et al., 2008) (see other measures in Table 1). Three techniques were used to investigate neurobiological substrates: functional magnetic resonance imaging (fMRI) (Cross et al., 2007; Lin et al., 2013, 2011; Wymbs and Grafton, 2009), diffusion magnetic resonance imaging (dMRI) (Song et al., 2012) and transcranial magnetic stimulation (TMS) (Kantak et al., 2011, 2010; Lin et al., 2008, 2011, 2009; Tanaka et al., 2010).

Eight studies were related to the following question: "Are there any differences in the participation levels of the PMA, M1, DLPFC or PPC across different practice schedules?" (Kantak et al., 2011, 2010; Lin et al., 2008, 2013, 2011, 2009; Tanaka et al., 2010; Wymbs and Grafton, 2009). Three studies were related to the question, "Throughout the practice process, does the involvement of the PMA, M1, DLPFC or PPC vary?" (Cross et al., 2007; Lin et al., 2013, 2011; Song et al., 2012). Five studies were related to the question, "What cognitive processes are employed during different practice schedules?" (Kantak et al., 2011, 2010; Lin et al., 2008, 2009; Tanaka et al., 2010). A summary of the above results is presented in Table 1.

Contextual interference effect was found in all of the studies that compared performance between blocked and random practice groups (Cross et al., 2007; Lin et al., 2008, 2013, 2011, 2009; Song et al., 2012; Tanaka et al., 2010). The variability of practice hypothesis was confirmed in the Kantak et al. (2010, 2011) study, which showed that the random variable practice groups exhibited improved performance relative to the constant practice groups.

Do the participation levels of the PMA, M1, DLPFC and PPC vary across different practice schedules? When comparing the roles of the DLPFC and the M1 in constant and random practice, it was found that the DLPFC is associated with motor-skill retention and transfer in random practice, whereas the M1 is associated with retention in constant practice (Kantak et al., 2011, 2010). Tanaka et al. (2010) observed that the M1 and SMA were not associated with random practice motor-skill retention. Conversely, the SMA was associated with blocked practice motor-skill retention. In all of the studies (Kantak et al., 2011, 2010; Tanaka et al., 2010), the regions that were investigated were contralateral to the dominant hand. Wymbs and Grafton (2009) observed that, by the end of the acquisition phase, random practice is associated with greater activation of the left PMA than blocked practice during movement preparation. During execution and also at the end of acquisition, random practice is associated with a greater level of activation in the right M1 and right PMC than blocked practice. Similar results were found by Lin et al. (2011, 2013), whose random practice group showed higher levels of functional connectivity during the acquisition phase and increased activation of the right DLPFC, right and left PMA and right PPC. During the retention test, a change in activation levels was observed, and the participants in the random group exhibited lower activation of the PMA and DLPFC than the participants in the blocked group. In analyzing motor evoked potential, a higher

Table 1
Variables related to the characteristics of the included studies.

Study	Task	Measure	Technique	Study purpose
Cross et al. (2007)	Press Key sequences	TAS; MT; KSA	fMRI	Examine the neural substrates involved in contextual interference during the acquisition phase.
Lin et al. (2008)	Aiming with reverse movements of elbow flexion and extension	RMSE	TMS	Investigate whether the forgetting-reconstruction hypothesis or the action-plan reconstruction hypothesis better explains the contextual interference effect.
Wymbs and Grafton (2009)	Press Key sequences	MT; RT	fMRI	Identify the neural substrates involved in random and blocked practice schedules.
Lin et al. (2009)	Aiming with reverse movements of elbow flexion and extension	TE; MAA	TMS	Investigate the relationship between contextual interference and processing spatial and temporal parameters in motor cortical areas.
Kantak et al. (2010)	Aiming with reverse movements of elbow flexion and extension	RMSE	TMS	Investigate the relationship between neural substrates that are involved in motor memory consolidation and practice schedules.
Tanaka et al. (2010)	Aiming sequences	TResp; MT; RE	TMS	Investigate the relationship between neural substrates that are involved in motor memory consolidation and practice schedules.
Lin et al. (2011)	Press Key sequence	TResp	fMRI; TMS	Investigate the neural basis of the contextual interference effect.
Kantak et al. (2011)	Aiming with reverse movements of elbow flexion and extension	RMSE	TMS	Investigate how the brain activity observed in skills consolidation contributes to learning transfer.
Song et al. (2012)	Press Key sequences	RT	dMRI	Investigate random practice effects in implicit learning and identify the correlations between changes in the microstructure of white matter and motor learning.
Lin et al. (2013)	Press Key sequences	TResp	fMRI	Identify the changes in functional connectivity in the DLPFC and PMC that are dependent on practice conditions.

MAA, movement amplitude accuracy; KSA, key sequences accuracy; RMSE, root mean square error; RE, response error; TE, timing error; TAS, time of analysis of sequence; MT, movement time; RT, reaction time; TResp, time of response.

level of M1 excitability was found in the random group during the acquisition phase (Lin et al., 2011). During acquisition, in both the preparation and execution of movements, the PPC was active in both random and blocked practice schedules (Cross et al., 2007; Wymbs and Grafton, 2009). Lin et al. (2011) found that the PPC was more bilaterally activated during acquisition in random practice than in blocked practice.

Throughout the practice process, does the involvement of the PMA, M1, DLPFC and PPC vary? During the acquisition phase, the random practice group exhibited increased activity during movement preparation in the PMC and M1 compared with the blocked group (Cross et al., 2007). There was also increased SMA and DLPFC activation during movement execution in the random practice group. When comparing the levels of M1 excitability from the beginning of the acquisition phase to the retention test, greater excitability was observed during the period in which motor skills were already consolidated, that is, during the retention test (Lin et al., 2011). The levels of functional connectivity in the PMC and DLPFC also varied throughout the acquisition phase during random practice, which was associated with better performance during the retention test. While changes in M1 white matter microstructure were associated with better learning during random practice, there were no specific changes during blocked practice (Lin et al., 2013; Song et al., 2012). At the end of acquisition, a higher level of activation in the right PPC was found in random practice versus blocked practice during movement execution (Wymbs and Grafton, 2009).

What cognitive processes are employed during different practice schedules? Lin et al. (2008) confirmed the elaborative-processing hypothesis, as in their study, M1 inhibition during the intertrial intervals of the acquisition phase of blocked practice did not generate sufficient forgetting and action plan reconstruction to produce the same level of learning as in random practice. While the performance levels of those who practiced in blocked sequences were unaffected by TMS, the higher level of task elaboration that was evoked by random practice was negatively affected by the stimulation. When comparing the effects of TMS on the spatial and temporal parameters of a task, only the temporal parameter was affected in random practice (Lin et al., 2009). The learning effects that occur during motor-skill retention and transfer in random practice appear to be mediated by the DLPFC, a region of the brain essential to human cognition. The same is not true in constant practice (Kantak et al., 2011, 2010). Similar results were found when comparing random and blocked practices. While the consolidation of motor skills in blocked practice was associated with SMA participation, such consolidation in random practice was not directly associated with motor areas (Tanaka et al., 2010). Details regarding the primary questions investigated in this study are presented in Table 2.

4. Discussion

Studies on the variability of practice and the contextual interference effect in motor learning began in the 1970s; since then, a great investigative effort has been made at the behavioral level. Integrating the behavioral and neurophysiological analyses of these issues is a quite recent development, taking into consideration that the earliest such study found was conducted by Cross et al. (2007). The current integrative review covered the theme "practice

Table 2
Details of the primary issues of study.

Study	Main behavioral outcomes	Main neurobiological outcomes
Cross et al. (2007)	In the acquisition phase, the blocked group was faster in time of analysis sequence (TAS) than the random group. There was no difference between groups with respect to movement time (MT). In the transfer test, the random group only had a lower TAS than the blocked group in tasks that were presented in a random order. In contrast, the random group had a lower MT than the blocked group only in tasks presented in a blocked order.	During the acquisition phase, fMRI analysis indicated neural substrates that were common to random and blocked practices in both the preparation (the right and left PMC, right and left SMA and left PPC) and execution of movements (the right and left M1, left PMC, right and left SMA, right DLPFC and right and left PPC). During the movement preparation phase, the regions involving the right PMC and right and left M1 exhibited increased activation levels throughout the practice session in the random group relative to the blocked group. During the movement execution phase, the right PMC and right SMA were more highly activated throughout the practice session in the random group than in the blocked group. fMRI analysis was not used in the transfer test.
Lin et al. (2008)	In the acquisition phase, between-trial TMS enhanced the performance of the blocked group versus that of the blocked control group. However, TMS had deleterious effects on the random group relative to the corresponding control group. In the delayed retention test, the random control group was superior to the blocked control group. However, there was no difference between the random and blocked groups that received TMS. The TMS random group showed a lower level of retention than the random control group. The same was not observed between the blocked practice groups.	The forgetting-reconstruction hypothesis was not confirmed, given that inhibiting the left M1 between trials during the acquisition phase did not enhance learning in the TMS blocked group versus the random group without TMS. The hypothesis that best explains the contextual interference effect is the elaborative-processing hypothesis. While TMS did not interfere with learning in the blocked group, it did disturb the high level of task elaboration that was evoked in the random practice group, thereby leading to lower levels of learning.
Wymbs and Grafton (2009)	During the acquisition phase, the blocked group was faster than the random group in measures of reaction (RT) and movement time (MT). During the retention test, the random group had a faster average MT than the blocked group. A comparison of the end of acquisition phase and retention test MTs indicated that offline learning occurred in the random group but not in the blocked group.	During the acquisition phase, in the movement preparation phase at the end of acquisition, random practice promoted a higher level of activation in the left PMC, left SMA and left PPC than did blocked practice. In the movement execution phase at the end of acquisition, random practice promoted a higher level of activation in the right M1, right PMC and right PPC than did blocked practice. The level of activation in the ipsilateral M1 (left hemisphere) at the end of acquisition was associated with motor performance in the retention test.
Lin et al. (2009)	During the acquisition phase, regardless of TMS, there was no difference between the random and blocked practice groups in timing error (TE). During the retention test, the random practice group without TMS had better performance with respect to TE than the blocked group without TMS. However, TMS had deleterious effects on the random group. There was no difference between the random and blocked groups with TMS. During the acquisition phase and retention test, there were no differences between groups with respect to movement amplitude accuracy.	The contextual interference effect presented a specific association with cortical motor activity. The disturbance generated by TMS over the left M1 affected only those who practiced in a random order; more specifically, it affected the temporal parameters of their movements. Intertrial intervals during the acquisition phase seem to be the central point of processing during random practice; a disturbance at the time of new parameter planning has a detrimental effect on learning.
Kantak et al. (2010)	The consolidation of practiced skills, as measured by root mean square error from the acquisition final phase to the retention test (offline learning), was higher in the random practice groups than in the constant practice groups.	TMS over the left M1 or left DLPFC after the acquisition phase leads to variable effects on the consolidation of motor memory. TMS over the M1 after random practice does not affect the consolidation of motor memory; however, TMS over the DLPFC deteriorates motor memory consolidation. Results opposite to the above were found for constant practice: TMS over the M1 deteriorated motor memory consolidation, but TMS over the DLPFC produced no deleterious effects.
Tanaka et al. (2010)	During the acquisition phase of experiment 1, wherein the groups had not suffered TMS, the blocked practice group had a faster time of response (TResp) than the random practice group. During the retention test of experiment 1, the blocked group that received TMS over the left SMA suffered a deleterious effect on TResp; the same did not occur following TMS in the random practice group.	While an association between random practice and neural substrate activation (M1, SMA and the dorsal region of the PMC) was not found during motor skill consolidation, the left SMA was associated with consolidation levels during blocked practice, mainly with the activation at the end of acquisition.

Table 2 (*Continued*)

Study	Main behavioral outcomes	Main neurobiological outcomes
	In experiment 2, it was observed that TMS over the left SMA affected TResp only if it was applied immediately after the acquisition phase. The application of TMS 6 h after the practice did not lead to a deterioration in learning in the blocked practice group. Random practice was not affected by TMS over the left M1 or over the dorsal region of the left PMC.	
Lin et al. (2011)	During the acquisition phase, the blocked group had a faster TResp than the random practice group.	During the acquisition phase, the random practice group had a higher level of bilateral activation than the blocked practice group in the M1, PMA, DLPFC and PPC.
	During the retention test, the random practice group performed better than the blocked group.	During the retention test, the random practice group had a lower level of activation than the blocked practice group in the right and left PMA, right DLPFC and right PPC.
	During the transfer test, there were no differences between the groups.	Analyzing the motor evoked potential following TMS application revealed increased M1 excitability in the random practice group during the acquisition phase compared with the blocked group. The level of M1 excitability during the retention test was greater than the excitability measured at the beginning of practice in the acquisition phase.
Kantak et al. (2011)	During the acquisition phase, there were no differences in performance between the random and constant practice groups.	TMS applied over the left DLPFC immediately after the acquisition phase disturbed the transfer of learning during random practice. Conversely, TMS applied over the left M1 after the acquisition phase perturbed the transfer of learning during constant practice. These results indicate that specific relationships exist between practice schedules, neural substrates and learning transfer.
	During the transfer tests, the random practice groups performed better than the constant practice group.	
Song et al. (2012)	During the acquisition phase, there were no differences between groups.	Changes in white matter microstructure during the acquisition phase were associated with performance during the retention test in both practice schedules (random and blocked).
	During the retention test, the random group had a faster average reaction time than the blocked group in each phase analyzed (immediately after practice and 12 h, 24 h and one week after acquisition).	More specifically, the better performance of the random practice group during the retention test was associated with structural connectivity changes in the left M1 and left PMC, while the performance of the blocked practice group during the retention test was associated with other brain regions.
Lin et al. (2013)	The blocked practice group had a faster TResp than the random practice group during the acquisition phase.	On the second day of the acquisition phase, random practice generated greater changes in functional connectivity between the right DLPFC and right PMC than blocked practice, with cortical (PPC and M1) and subcortical regions being involved in the planning and execution of motor skills.
	During the retention test, the random group had a faster TResp than the blocked group.	Random practice led to greater connectivity in the right DLPFC and right PMC, which was associated with better performance during the retention test that was administered 3 days after the end of the acquisition phase. During the retention test, increased connectivity between the DLPFC and SMA was observed, which was correlated with the benefits of random practice.

schedule" by focusing on articles that were published in scientific journals with a neuroscience scope (Cross et al., 2007; Kantak et al., 2010; Lin et al., 2013, 2011; Song et al., 2012; Tanaka et al., 2010), thereby going beyond traditional journals dedicated to behavioral studies.

Regarding the motor tasks that were evaluated, a common feature among the studies was the use of sequential tasks that were subdivided into key-press-based tasks (Cross et al., 2007; Lin et al., 2011; Song et al., 2012; Wymbs and Grafton, 2009) and sequential aiming tasks (Kantak et al., 2011, 2010; Lin et al., 2008, 2009; Tanaka et al., 2010). Traditional behavioral measurements were used, such as reaction time (Song et al., 2012; Wymbs and Grafton, 2009), movement time (Cross et al., 2007; Tanaka et al., 2010; Wymbs and Grafton, 2009), time of response (Lin et al., 2013, 2011; Tanaka et al., 2010; Wymbs and Grafton, 2009) and root mean square error (Kantak et al., 2011, 2010; Lin et al., 2008). The techniques for evaluating neural correlates concentrated on fMRI (Cross et al., 2007; Lin et al., 2013, 2011; Song et al., 2012; Wymbs and Grafton, 2009) and TMS (Kantak et al., 2011, 2010; Lin et al., 2008, 2011, 2009; Tanaka et al., 2010).

Do the participation levels of the PMA, M1, DLPFC and PPC vary across different practice structures? A variety of evidence suggests an affirmative answer to this question. The application of TMS to the M1 during intertrial intervals disrupts processing during random practice, consequently affecting learning. The same does not occur with blocked practice (Lin et al., 2008, 2009). More specifically, this perturbation has a greater negative effect on temporal parameter learning than on spatial parameter learning (Lin et al., 2009).

During random practice, the DLPFC was found to be highly associated with motor-skill retention and transfer, whereas retention and transfer during constant practice had a greater association with M1 activation (Kantak et al., 2011, 2010). Tanaka et al. (2010) also observed a difference between practice schedules: blocked practice was more associated with SMA activation during skills consolidation than was random practice. At the end of the acquisition phase, there was greater activation of the DLPFC and premotor areas (PMC and SMA) during movement preparation in random practice than in blocked practice. During the movement execution period and also at the end of the acquisition phase, random practice induced greater M1 and PMC activation than blocked practice. Lin et al. (2011, 2013) found similar results. In their study, during acquisition, the random practice group showed higher activation in the DLPFC and premotor areas. An opposite effect was observed during the retention test, wherein the random practice group had diminished activation in the DLPFC and premotor areas. Moreover, analysis of the motor evoked potential showed greater M1 excitability in the random group during the acquisition phase (Lin et al., 2011).

Throughout the practice process, does the involvement of the PMA, M1, DLPFC and PPC vary? Changes in the neural circuits involved in motor representation formation show that when a skill is well learned and asymptotic performance is reached, skill representation can be distributed through a network of structures involving cortico-striatal or cortico-cerebellar circuits, depending on the type of learning experienced. Unlike studies of motor adaptation, studies on practice organization require a learner to acquire one or more motor skills. Thus, throughout learning, there is decreased participation of the cortico-cerebellar system, while the cortico-striatal system participates more effectively during the final phase of skill acquisition. When skill consolidation is evaluated by a retention test, it is also expected that the cortico-striatal system is reactivated (Doyon et al., 2003).

Our proposition that the participation of the cortico-striatal system increases at the end of acquisition and during retention testing is supported by the results of the included studies. Cross et al. (2007) observed a common pattern of activation of the cerebellum and basal ganglia during acquisition in both random and blocked practice groups. However, there was decreased activity in the cerebellum during random practice versus blocked practice at the end of acquisition. Superior skill consolidation in random practice is correlated with the structural connectivity of the sensorimotor cortico-striatal loop (Song et al., 2012). Lin et al. (2013) found an increase in functional connectivity between the caudate nucleus (one of the basic structures of the basal ganglia) and the DLPFC from the first day to the second day of random practice. Moreover, this functional connectivity was maintained during a retention test that was applied 3 days after practice. During the encoding phase, random practice facilitates prefrontal-basal ganglia connectivity, and this connectivity is maintained after memory consolidation.

In analyzing specific cortical areas, our integrative literature review indicated that different processes are associated with random and blocked practices. A consensus among studies was found in our movement preparation analysis: random practice promotes increased activity in the PMC throughout practice (Cross et al., 2007; Wymbs and Grafton, 2009). While Wymbs and Grafton (2009) also noted increased activity in the SMA and PPC, areas well known to be involved in planning, during random practice, Cross et al. (2007) found increased M1 activity throughout random practice, unlike during blocked practice. Despite the similarities of the tasks, such as their sequential characteristics, the constraints applied during the preparation period differed between these studies. The length of time provided for learners to prepare their response was unrestricted in the Cross et al. (2007) study, leading to the question of whether the participants would engage in some form of mental practice before movement execution. It has been observed that the M1 participates in mental imagery (Feurra et al., 2011; Lotze et al., 1999). Regarding the movement execution phase, increased levels of activity in the SMA (Cross et al., 2007), PMC, M1 and PPC (Wymbs and Grafton, 2009) were observed during random practice over the course of acquisition. An overall analysis of these results shows that the structures involved in the planning and execution of skills tend to exhibit greater increases in activity during random practice than during blocked practice. The best consolidation of skills that was observed during random practice was associated with increased motor area activity at the end of the acquisition phase. The opposite effect was observed during retention testing. When assessing the effects of skills consolidation, random practice has been associated with lower levels of activation in premotor areas and the DLPFC than blocked practice (Lin et al., 2011). The analysis of cortical excitability also demonstrated that the participation levels of the motor regions of the brain during acquisition are associated with performance quality during learning tests. When comparing M1 excitability levels at the beginning of the acquisition phase to those during the retention test, an increase was observed only for the random practice group (Lin et al., 2011). Structural and functional connectivity levels also changed throughout practice. For example, changes in M1 white matter microstructure were associated with better retention in the random practice group (Lin et al., 2013; Song et al., 2012).

In addition to motor region activation, Cross et al. (2007) observed a higher level of DLPFC activation at the end of acquisition in the random practice group. On the second day of random practice, DLPFC activation was more highly associated with sensorimotor planning regions, including the PPC and cerebellum, than on the first day of practice (Lin et al., 2013). Motor task variation between trials required the activation of the DLPFC, a region that is central to executive function. Conversely, the consecutive repetition of a motor task resulted in decreased DLPFC activity (Rushworth et al., 2005, 2002). The participation of the DLPFC during off-line consolidation processes and skills recovery seems to be central to random practice (Kantak et al., 2010; Lin et al., 2013), while M1 participation is crucial to practice schedules that require repetition (Kantak et al., 2010). Variation seems to demand more of a planning process and working memory involving the DLPFC than does repetitive practice. It is possible that a higher level of variation produces a stronger relationship between processes involving a goal component and an action component in movement. In contrast, a more repetitive schedule of practice requires more of an action component in movement, creating a weaker relationship between these processes.

In summary, the absence of the consecutive repetition of a given skill during a random execution sequence leads to poorer learning performance than does experiencing a sequence in blocks (Shea and Morgan, 1979). However, the poor performance levels of those who practice in a random order masks the greater psychophysiological demands that this type of condition requires. The participation of brain regions involved in executive control and in motor skill planning and execution increases throughout practice, and this increased participation, which is reflected by a higher activation level and cortical excitability, is a critical factor in learning consolidation (Fig. 5).

What cognitive processes are employed during different practice schedules? The results of the analyzed studies offer empirical support for behavioral hypotheses that suggest greater cognitive engagement during random practice. Subcortical structures exhibited higher levels of activation during movement preparation at the end of acquisition during blocked practice. Conversely, areas directly associated with motor planning were most active during random practice (Wymbs and Grafton, 2009). Movement execution conditions that have a repetitive nature seem to require less engagement in the planning and organization of motor skills.

The greater cognitive engagement observed during random practice may be due to the higher levels of elaboration and distinction that are involved in processing (Shea and Zimny, 1983) or may be generated by forgetfulness and action plan reconstruction (Lee and Magill, 1983). Lin et al. (2008, 2009) proposed a design to test these hypotheses: they applied TMS to the M1 between trials, which could produce two types of results. If forgetting and reconstruction is the process responsible for the higher level of learning during random practice, then a blocked practice group subjected to TMS should generate similar levels of learning as a random practice group without TMS. The inhibition generated by TMS forces a learner to rebuild a plan of action between trials,

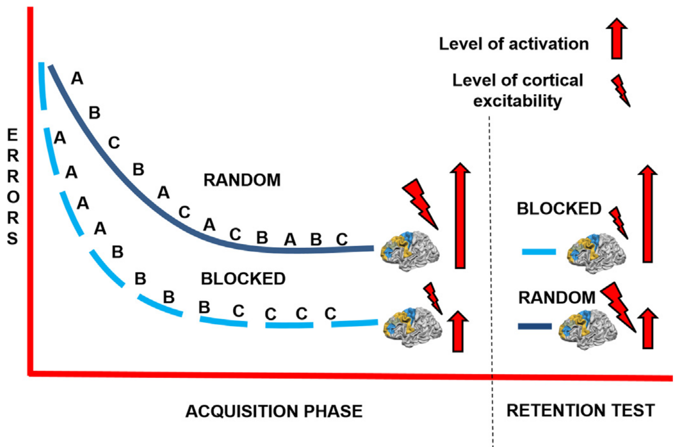

Fig. 5. Performance skills of the random and blocked practice groups and their corresponding levels of cortical activation and excitability. Compared with blocked practice, random practice promotes poorer performance during the acquisition phase. However, physiological processes occur in key cortical areas for learning, favoring the retention of the practiced skills.

causing a process similar to that experienced during random practice. Conversely, if a higher level of distinction and elaboration is the predominant mechanism, the level of learning capacity of a blocked practice group should not be affected by TMS, while a random practice group subjected to TMS should exhibit decreased learning. The second possibility was confirmed. The higher level of distinction and elaboration in the tasks evoked by random practice was negatively affected by TMS, confirming the elaborative-processing hypothesis (Shea and Zimny, 1983). A critical analysis regarding these findings of Lin et al. (2008, 2009) is that the results can only reflect M1's critical role in random practice-mediated learning, but not necessarily supports the elaborative-processing hypothesis.

An important aspect that still needs to be investigated to clearly define which is the best hypothesis is the role of the DLPFC during this process, similar to the investigation of the role of the M1 by Lin et al. (2008, 2009). Working memory functions allowing the maintenance and manipulation of online information are associated with DLPFC activation (Diamond, 2000; Nee et al., 2012). These functions seem to be required more during non-systematic practice than during repetitive practice. Lin et al. (2013) found that increased connectivity between the SMA and DLPFC during random practice is associated with better retrieval of motor skills from memory. While the consolidation of skills during constant (Kantak et al., 2010) and blocked (Tanaka et al., 2010) practices is more highly associated with the participation of motor areas only, the consolidation and recovery of skills during random practice is also associated with regions involved in executive control, specifically the DLPFC. It is possible that a new plan of action needs to be produced when the DLPFC is inhibited between trials, but not when the M1 is inhibited. Thus, one possible method of comparing the two behavioral hypotheses would be the application of TMS to the DLPFC between trials to assess whether this area is related to action plan reconstruction. As opposed to M1 inhibition (Lin et al., 2008, 2009), the inhibition of DLPFC by TMS has the potential to force a learner to rebuild a plan of action between trials during blocked practice, thereby promoting a similar level of learning as in random practice.

The elaborative-processing and forgetting-reconstruction hypotheses are commonly investigated as excluding propositions; however, it is possible that random practice can be affected by both processing mechanisms. The differences between the studies by Shea and Zimny (1983) and Lee and Magill (1983) appear to be reconcilable. Shea and Zimny (1983) highlight that an error of execution might stimulate a learner to engage in additional processing. The process of error correction might induce the reconstruction of a new motor sequence. The use of multiple processing strategies and the variable use of these strategies can not only produce high levels of intratask and intertask comparisons between trials but also enable the forgetting and reconstruction of new action plans. The potential reconciliation of these hypotheses to explain the benefits of random practice versus blocked practice would pose a novel challenge to researchers investigating practice organization from a neuroscience perspective.

5. Conclusion

In conclusion, during different practice schedules, there is varied participation of the PMA, M1, DLPFC and PPC. For example, the M1 is more active and excitable throughout the acquisition phase of random practice than during practice schedules that have a repetitive nature. The participation levels of the indicated areas change throughout the process of practice. There is greater activation of neural structures involved in the planning and execution of skills during the acquisition phase of random practice than during blocked practice. The opposite effect is observed in retention testing, during which random practice leads to decrease levels of activation in the indicated regions.

Regarding the cognitive processes that are involved in different practice schedules, evidence found in the literature points to greater engagement during random practice. However, further study is required to investigate whether the benefits provided by random practice are related to higher levels of elaboration and distinction of the practiced skills or to the processes of forgetfulness and action plan reconstruction. In conclusion, the integration of behavioral and neurophysiological findings promotes a broad view of the phenomenon of practice organization.

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