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Declarative interference affects off-line processing of motor imagery learning during both sleep and wakefulness

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ABSTRACT

Retroactive interference from a declarative memory can prevent the consolidation of motor skill memories over wakefulness, but not over a night of sleep. Recently, motor imagery (MI) learning has been showed to allow for a stronger resistance against procedural interference rather than physical practice, but whether declarative interference might impact sleep-dependent consolidation process of an explicit finger tapping task learned with MI remains unknown. To address this issue, 57 subjects mentally rehearsed an explicit finger tapping sequence, and half of them were then requested to practice an interferential declarative task. All participants were re-tested on the initial procedural task either after a night of sleep or a similar daytime interval. The main findings provided evidence that declarative interference affected MI consolidation both over the night- and wakefulness intervals. These results extend our previous findings by underlying that declarative interference might impact more strongly explicit MI practice than physical practice, hence suggesting that MI might rely on declarative memory rather than exclusively on procedural memory system. The relationship between declarative and procedural memories during MI practice, as well as during off-line consolidation, is discussed.

1. Introduction

Memory is commonly divided into declarative and procedural memory systems (Cohen & Squire, 1980). Declarative memory is accessible to conscious recollection, i.e. memories for events in a spatio-temporal context (episodic memory) and fact based information (semantic memory). Procedural memory rather includes a heterogeneous collection of abilities resulting from experiences being not necessarily available for conscious recollection. The acquisition of declarative memories is usually intentional, with an individual's awareness (explicit learning), while the acquisition of procedural skills can be accomplished unintentionally, with little awareness (implicit learning), or explicitly (Shanks & St. John, 1994). Following the acquisition of the learning material, consolidation takes place automatically, without awareness, and allows the conversion of the initial unstable memory representation into a more stable and effective form (Stickgold & Walker, 2007). A substantial number of studies demonstrated that additional offline improvements in both declarative and procedural memories might occur after a night of sleep (Fischer, Hallschmid, Elsner, & Born, 2002; Korman, Raz, Flash, & Karni, 2003; Korman et al., 2007; Robertson, Pascual-Leone, & Press, 2004; Stickgold & Walker, 2005; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker et al., 2003). In particular, Robertson et al. (2004) investigated whether the implicit–explicit distinction of a sequential finger tapping task (FTT) influenced offline learning. They demonstrated that performance gain was sleep-dependent for explicit procedural learning but time-dependent for implicit skills, hence suggesting that procedural memory consolidation processes may depend on the nature of the task acquisition.

During the post-learning phase of the consolidation process, the establishment of long-term memory can be blocked by chemical, electrical or behavioral interference (Krakauer & Shadmehr, 2006; McGaugh, 2004; Shadmehr & Holcomb, 1997; Walker & Stickgold, 2004). Accordingly, behavioral interference describes a case in which the consolidation of a primary task is substantially disrupted by immediately performing a secondary task. This process is usually called retroactive interference (Brashers-Krug, Shadmehr, & Bizzi, 1996; Walker, Brakefield, Hobson, & Stickgold, 2003). Until the last 10 years, declarative memory has been thought to be processed and retained within a set of neural circuits

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that are independent from neural networks responsible for processing and retaining procedural memory (Cohen & Squire, 1980). Memory interference paradigms have helped to reshape our understanding of how memories are organized within the human brain by demonstrating the processing of declarative and procedural memories systems (Robertson, 2012). A large body of research examined such kind of interference within the same memory system (i.e. procedural or declarative). For example, learning a mirror-reversed FTT (interference) 2 h of rest period after the initial FTT prevented the expression of delayed gains at 24 h post-training. In contrast, allowing 8 h of rest period before learning an interfering FTT did not prevent from delayed performance gains 24 h post-training (Korman et al., 2007). It is worthwhile noting that when the procedural interfering task is not related to that of the initial motor learning, but is performed with the same limb, interference occurs (for example see Balas, Netser, Giladi, & Karni, 2007). So far, recent studies showing interference between declarative and motor skill memories have challenged the concept of independent memory systems. In a seminal study, Brown and Robertson (2007b) modified those type of encapsulated memory protocols by examining the interference between the declarative and procedural systems when consolidation takes place over wake or over a night of sleep. They reported that the off-line consolidation of an implicit procedural memory can be blocked by declarative learning, while the off-line processing of a declarative memory might be blocked by implicit procedural learning as well. Interestingly, this reciprocal interaction between memory systems was observed over wakefulness, but not after a night of sleep. They further concluded on the existence of a dynamic relationship between memory systems modulated by when consolidation takes place, allowing reciprocal interaction to occur in certain situations. These findings are consistent with the current observations suggesting that memory systems interact during wakefulness and operate independently during sleep (Diekelmann, Buchel, Born, & Rasch, 2011; Robertson, 2009), which could be explained by changes in functional connectivity among different brain areas elicited once the brain shifts from wake to sleep (Massimini et al., 2005).

In the wealth of the mental practice literature, motor imagery (MI) is a reliable complement to physical practice in enhancing cognitive and motor performance (Guillot & Collet, 2008), hence promoting the consolidation process toward the long term memory system (Jackson, Lafleur, Malouin, Richards, & Doyon, 2001). MI is a dynamic state during which an individual mentally simulates the performance of an action, without any overt body movement (Decety, 1996; Jeannerod, 1994). With regards to physical practice, MI offers the advantage to be cost-effective and easily feasible (Guillot & Collet, 2005). Several models support that MI is effective in strengthening the memory trace for a motor skill, suggesting a causal link between MI and motor memory consolidation (Murphy, Nordin, & Cumming, 2008). A further important distinction has been made between tasks that explicitly ask subjects to perform MI (e.g. FTT) and those where imagined actions are implicitly, but not necessarily, engaged (e.g. mental rotation, Jeannerod & Frak, 1999). Accordingly, the effects of MI on the improvement of procedural skill learning are now well-established (Feltz & Landers, 1983), including explicit FTT tasks (Debarnot, Clerget, & Olivier, 2011b; Debarnot, Creveaux, Collet, Doyon, & Guillot, 2009a; Lacourse, Turner, Randolph-Orr, Schandler, & Cohen, 2004). There is now ample evidence that MI and physical practice share several characteristics at temporal, behavioral and neural levels (Holmes & Collins, 2001; Munzert, Lorey, & Zentgraf, 2009). Practically, similar performance gains have been observed after a night of sleep when participants practiced MI compared to physical practice of an explicit FTT, while a comparable time interval during daytime did not affect motor memory consolidation (Debarnot, Castellani, Valenza, Sebastiani, & Guillot, 2011a; Debarnot et al., 2009a). These results further reinforced the principle of functional equivalence between MI and physical practice, by demonstrating sleep related effects on motor memory consolidation following MI. Based on these findings and on the study by Korman et al. (Korman et al., 2007), Debarnot, Maley, De Rossi, and Guillot (2010) investigated whether an explicit procedural interference could impact motor consolidation after a 2 h rest interval following an explicit MI practice task as compared to that following physical practice. They demonstrated that explicit MI practice resulted in less retroactive interference than physical practice of the same task, and outlined the relevance of the first night of sleep for the consolidation process following MI practice. Since it has been stated that, compared to physical practice, MI would result in an effector-independent representation (Wohldmann, Healy, & Bourne, 2008), then we can speculate that the explicit memory trace elicited with MI practice might rely on declarative memory system rather than exclusively on procedural.

Overall, despite accumulated evidence that memory systems interact (Brown & Robertson, 2007a,b; Keisler & Shadmehr, 2010), there is yet no experimental data about that relationship when procedural learning is done with MI. Hence, the main objective of the present study was twofold: (i) determining whether motor consolidation following explicit MI practice of a FTT can be disrupted by declarative learning interference, and (ii) examining whether a night of sleep might *protect* the initial motor learning from the interfering effects of the declarative task. To do so, we evaluated the effect of a declarative interference after an explicit MI learning, 12 h after a night- or day-time consolidation. During recent years, MI has received increasing attention as a valuable training approach in rehabilitation of stroke patients (de Vries & Mulder, 2007; Dijkerman, Ietswaart, Johnston, & MacWalter, 2004; Sharma, Pomeroy, & Baron, 2006). So far, it has been underlined that designing effective imagery interventions depends on patients' intentions, and imagery content (Schuster, Glassel, Scheidhauer, Ettlin, & Butler, 2012). Therefore, exploring in greater detail the effect of retrograde interference on MI practice might shed light on how optimally scheduling and using MI efficiently in rehabilitation programs.

2. Materials and methods

2.1. Participants

Fifty-seven healthy volunteers (37 women, age range: 20–35, mean ± SD: 23.96 ± 3.32) participated in this experiment and were evenly distributed into four independent groups relative to the application of interference and the consolidation interval: Interference-Night ($n = 16$), Interference-Day ($n = 15$), Control-Night (without interference, $n = 12$) and Control-Day ($n = 14$). All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They reported sleeping regularly between 7 and 9 h per night, and extreme evening- and morning-type individuals, as well as regular nappers and smokers, were excluded. None had any prior history of drug or alcohol abuse, neurological, psychiatric, or sleep disorders, and they were instructed to be drug, alcohol, and caffeine free for 24 h prior, and during the experiment. Musicians and professional typists were excluded to avoid participants with previous experience on FTT. This study was approved by the local Research Ethics Committee, and all participants signed an informed consent form. The procedure was explained and instructions regarding the motor task and questionnaires were given, while no information was provided about the objectives of the study, or the dependent variables of interest.

Before the experiment, all participants were first asked to fill out the Pittsburg Sleep Quality Index to assess sleep quality and