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Research report

Offline consolidation in implicit sequence learning

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ABSTRACT

The goal of this study was to investigate offline memory consolidation with regard to general motor skill learning and implicit sequence-specific learning. We trained young adults on a serial reaction time task with a retention interval of either 24 h (Experiment 1) or 1 week (Experiment 2) between two sessions. We manipulated sequence complexity (deterministic *vs* probabilistic) and motor responses (unimanual or *vs* bimanual). We found no evidence of offline memory consolidation for sequence-specific learning with either interval (in the sense of no deterioration over the interval but no further improvement either). However, we did find evidence of offline enhancement of general motor skill learning with both intervals, independent of kind of sequence or kind of response. These results suggest that general motor skill learning, but not sequence-specific learning, appears to be enhanced during offline intervals in implicit sequence learning.

1. Introduction

There have been a vast number of studies on sequence learning, but only recently has there been much interest in how it relates to memory consolidation. The term consolidation usually refers to the *stabilization*, and even *enhancement*, of memory traces after their initial acquisition. For example, it has been demonstrated that the performance of some procedures can be significantly improved after a "silent" or *offline* interval subsequent to training. During this interval, there is no further practice, or even mention, of the procedure, and learning remains largely tacit or *implicit* (Brown & Robertson, 2007; Hallgato, Gyori-Dani, Pekar, Janacsek, & Nemeth, 2013; Krakauer & Shadmehr, 2006; Németh et al., 2010). Consolidation is also sometimes referred to as *resistance* to interference and forgetting (Ghilardi, Moisello, Silvestri, Ghez, & Krakauer, 2009; Goedert & Willingham, 2002; Stephan, Meier, Orosz, Cattapan-Ludewig, & Kaelin-Lang, 2009). In the present study, we use the first definition (i.e., further improvement or enhancement). For related reviews see Doyon et al. (2009), Robertson (2009), Siengsukon and Boyd (2009), and Song (2009). Q2

Offline consolidation of sequence learning may depend on a variety of factors, such as training session intervals (Albouy et al., 2008; Press, Casement, Pascual-Leone, & Robertson, 2005; Walker, Brakefield, Hobson, & Stickgold, 2003), practice (Korman, Raz, Flash, & Karni, 2003; Shanks & Cameron, 2000; Steele & Penhune, 2010), sleep versus wakefulness and time of day (Brawn, Fenn, Nusbaum, & Margoliash, 2010; Cajochen et al., 2004; Della-Maggiore, 2005; Doyon et al., 2009; Fischer, Hallschmid, Elsner, & Born, 2002; Keisler, Ashe, & Willingham, 2007; Kuriyama, Stickgold, & Walker, 2004; Manoach et al., 2004; Maquet, Schwartz, Passingham, & Frith, 2003; Peigneux et al., 2003; Spencer, Sunm, & Ivry, 2006), and degree of explicit awareness (Ghilardi et al., 2009; Hotermans, Peigneux,

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Maertens de Noordhout, Moonen, & Maquet, 2006; Robertson, Pascual-Leone, & Press, 2004). It is not yet clear how sequence learning *per se* changes from a labile state to a more stable one, although there is a large body of work on motor memory consolidation (see Krakauer & Shadmehr, 2006, for a review).

The purpose of the present study was to investigate the separate contributions of general motor skill learning and sequence-specific memory consolidation in *implicit* sequence learning. General motor skill learning refers to faster responses as a result of practice. Sequence-specific learning refers to faster responses as a result of the acquisition of sequence-specific knowledge. Many serial reaction time task (SRTT) studies to date have not distinguished between these two components of performance (but see Hallgato et al., 2013; Németh et al., 2010; Song, Howard, & Howard, 2007, for exceptions).

Evidence of offline motor memory consolidation in conjunction with *explicit* sequence learning was found when participants performed a finger-tapping task with two training sessions (Doyon et al., 2009; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Brakefield, Seidman, et al., 2003). Specifically, after one night's sleep, with no further practice between sessions, participants showed marked improvements in speed and accuracy. However, there is a difference between motor skill learning in a finger-tapping task of this kind, with short, simple response sequences, and implicit sequence learning in a SRTT, with longer, more complex sequences. In the former, measures of performance relate to the speed at which the movements are carried out, that is, general motor skill. In the latter, measures of performance relate to both the speed of the movements, but also to sequence-specific learning. Beneficial changes in performance that occur during training are taken as evidence of *online learning* of both motor skill learning and sequence-specific learning. Additional improvements, that develop during intervals between sessions, in the absence of further physical practice, are taken as evidence of *offline consolidation* (Krakauer & Shadmehr, 2006; Robertson et al., 2004). The terms are sometimes confused as well as confounded.

Research into motor memory consolidation suggests that implicit sequence learning might be stabilized during the hours immediately after learning, which would be compatible with the time course of synaptic change (Morris, 2006). However, there is, as yet, no firm evidence of an offline consolidation process for *implicit* sequence-specific learning. In contrast, this occurrence has been well documented for *explicit* sequence learning (Press et al., 2005; Walker et al., 2002). It may well be that whereas sleep is helpful towards the consolidation of explicit memory traces (i.e., *passive* offline processing), sufficient practice (i.e., *active* online training) is all that is useful for the consolidation of implicit memory traces (Della-Maggiore, 2005; Press et al., 2005; Robertson et al., 2004; Walker, Brakefield, Hobson, et al., 2003). In fact, offline consolidation, in the sense of "silent" improvement, may play no role at all in implicit sequence-specific learning (Hallgato et al., 2013; Németh & Janacsek, 2011; Németh et al., 2010; Siengsukon & Boyd, 2009; Song et al., 2007; Spencer, Gouw, & Ivry, 2007).

For example, when learning was assessed in young adults across three sessions with equivalent intervals of wakefulness or sleep, Song et al. (2007) found offline improvement in motor skill learning after wakefulness but not sleep. Further, when Németh et al. (2010) used an alternating serial reaction time task (ASRTT, see Howard & Howard, 1997; Romano, Howard, & Howard, 2010), they found no sequence-specific improvements from an a.m. to p.m. session or a p.m. to a.m. session. Similarly, when Németh and Janacsek (2011) tested participants on *probabilistic* sequence learning, before and after a 12-h, 24-h, or a 1-week interval, they found an improvement in general motor skill (i.e., motor learning regardless of sequencing) in young adults after all three intervals (older adults only showed improvement after the 12-h interval). Q3 Importantly, Németh and Janaseck found no improvement in *sequence-specific learning* in either age group after any of the intervals.

The purpose of this study was to investigate offline consolidation of motor skill learning and sequence-specific learning in the sense of improvements in learning rather than just stabilization or lack of deterioration. We report two experiments, in which an SRTT was used. In Experiment 1, consolidation was tested after an interval of 24 h and in Experiment 2, consolidation was tested after one week. In both experiments, one half of the participants were exposed to a *deterministic* sequence and the other half to a *probabilistic* sequence. To test probabilistic sequence learning we used an ASRTT in which every alternate component is sequenced according to a predictable rule with pseudorandom trials in between (see Howard & Howard, 1997; Németh et al., 2010; Romano et al., 2010). The main reason for using a *probabilistic* sequence was to avoid the emergence of explicit knowledge, which might alter performance (Cleeremans & Jiménez, 1998; Destrebecqz & Cleeremans, 2001; Perruchet, Bigand, & Benoit-Gonin, 1997; Remillard, 2008; Remillard & Clark, 2001; Song et al., 2007). We tested whether consolidation would differ for the learning of probabilistic and deterministic sequences, in particular, whether it might be stronger for deterministic sequences (see Deroost, Zeeuws, & Soetens, 2006; Destrebecqz & Cleeremans, 2001; Wilkinson & Jahanshahi, 2007). In fact, it has been shown that when sequence structure is complex, as it is for probabilistic sequences, offline consolidation of sequence learning may not occur (Goedert & Willingham, 2002), or at least not unless the sequence is explicit and not without an interval including sleep (see Cohen & Robertson, 2007; Song, 2009).

In both experiments presented here, responses were either *bimanual*, with half of the participants in each condition using the index and ring fingers of both hands, or *unimanual* with the other half of the participants using all four fingers of the dominant hand. We reasoned that, as information would be integrated across the left and right brain hemispheres, consolidation of bimanual learning might be enhanced compared to unimanual. Indeed, after an interval of 24 h, Kuriyama et al. (2004) found enhanced consolidation in *bimanual* compared to *unimanual* finger-tapping performance, but this was only when the sequence was complex. A number of fMRI studies have shown that bimanual and unimanual tasks recruit somewhat different neural systems in the early stages of motor training, but it is not yet clear if this has any lasting effect on memory consolidation in sequence-specific learning (Bapi, Doya, & Harner, 2000; Gerloff & Andres, 2002; Sun, Miller, Rao, & D'Esposito, 2007). Q4

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