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Review

Implicit sequence learning and working memory: Correlated or complicated?

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ABSTRACT

The relationship between implicit/incidental sequence learning and working memory motivated a series of research because it is plausible that higher working memory capacity opens a “larger window” to a sequence, allowing thereby the sequence learning process to be easier. Although the majority of studies found no relationship between implicit sequence learning and working memory capacity, in the past few years several studies have tried to demonstrate the shared or partly shared brain networks underlying these two systems. In order to help the interpretation of these and future results, in this mini-review we suggest the following factors to be taken into consideration before testing the relationship between sequence learning and working memory: 1) the explicitness of the sequence; 2) the method of measuring working memory capacity; 3) online and offline stages of sequence learning; and 4) general skill- and sequence-specific learning.

Although implicit sequence learning is a subconscious process which is believed to be independent from general cognitive resources such as working memory (WM), in the past few years several studies have set out to demonstrate the shared or partly shared brain networks underlying these two systems. For example, disrupting the dorsolateral prefrontal cortex (DLPFC), a structure involved in WM, with transcranial magnetic stimulation (TMS) impairs implicit sequence learning (Pascual-Leone et al., 1996; Robertson et al., 2001). However, the role of PFC in implicit sequence learning is controversial: while some studies found activation of the DLPFC in implicit sequence learning (Pascual-Leone et al., 1996; Robertson et al., 2001; Schwarb and Schumacher, 2009), others failed to find such a relationship (Bo et al., 2011b; Fletcher et al., 2005; Rieckmann et al., 2010). Moreover, several studies showed that manipulations reducing the dominance of the PFC and/or the medial temporal lobe (MTL), such as a demanding secondary task (Foerde et al., 2006), a distractor task inserted between the learning sessions (Brown and Robertson, 2007), hypnosis during learning (Nemeth et al., 2013) or neuropharmacological blockage (Frank et al., 2006), had no effect or even led to performance improvements in sequence learning tasks. These latter findings support the competitive nature of the PFC- and MTL-dependent

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and basal ganglia-dependent memory systems (Poldrack et al., 2001).

To refine the interpretation of these and future results, we outline several factors in this mini-review to be taken into consideration before planning brain imaging, psychophysiology, and behavioral studies on the relationship between sequence learning and WM.

1. Evidence for independence between implicit sequence learning and WM

The relationship between implicit sequence learning and WM motivated a series of research because it is plausible to suggest that higher WM capacity opens a "larger window" to a sequence, allowing thereby the sequence learning process to be easier (Frensch and Miner, 1994; Howard and Howard, 1997). However, the majority of studies (see Table 1) found no relationship between implicit sequence learning and WM capacity. For instance, Feldman et al. (1995) demonstrated that there is no significant correlation between sequence learning scores (performance on a random block minus performance on a sequence block) on a 10-element deterministic implicit serial reaction time (SRT) task and span tasks (Digit and Backward Digit Span Tasks; and Wisconsin Card Sorting Test). Unsworth and Engle (2005) found that high and low WM capacity individuals (measured by Operation Span Task) did not differ in performance on implicit sequence learning; moreover, the implicit sequence learning was independent from general fluid intelligence. Kaufman et al. (2010) found similar results using a probabilistic implicit sequence learning task and demonstrated with structural equation modeling that WM is independent from implicit learning. Frensch and Miner (1994) also failed to find a significant correlation between implicit/incidental sequence learning in the single-task condition and performance on span tasks. Bo et al. (2011a, 2012) did not find a correlation between classical learning score on the SRT task and WM measures either.

Neuropsychological investigations also suggest the independence of implicit sequence learning and WM. For example, a recent study found WM deficits, but intact implicit sequence learning abilities in individuals with Obstructive Sleep Apnea (Nemeth et al., 2012). In addition, several studies showed intact implicit sequence learning in groups with intellectual disabilities, for example in Autistic Spectrum Disorder (Barnes et al., 2008; Brown et al., 2010; Nemeth et al., 2010a) or Down-Syndrome (Vicari et al., 2007). As WM is highly correlated with general intellectual abilities while implicit learning is independent of IQ (e.g., Kaufman et al., 2010), we can interpret these results as indirect evidence for independence between implicit sequence learning and WM. In sum, despite partly overlapping brain networks (Pascual-Leone et al., 1996; Sefcsik et al., 2009), these two systems seem to be separate from each other on the functional level.

2. Factors influencing effects of WM on sequence learning

2.1. *Explicitness of the sequence*

If the sequence learning is explicit/intentional, WM differences emerge in the sequence learning tasks (Unsworth and

Table 1 – Studies investigating the relationship between sequence learning and WM. "Mixed" indicates when general skill and sequence-specific learning cannot be separated in the analysis method that the study used.

Study	Explicit/implicit	WM measure	Online/offline	General skill/sequence-specific	WM effect
Frensch and Miner (1994), Exp. 1	Explicit	Span task	Online	Sequence-specific	Yes
	Implicit				No
Frensch and Miner (1994), Exp. 2	Implicit	Span task, dual-task condition	Online	Sequence-specific	Yes
Feldman et al. (1995)	Implicit	Span task	Online	Sequence-specific	No
Howard and Howard (1997)	Implicit	Span task	Online (Session 1)	Sequence-specific	Not analyzed separately
			Online + offline (Session 1–6)		Yes
Schwartz et al. (2003)	Implicit	Span task	Online (Session 1)	Sequence-specific	No
			Online + offline (Session 1–6)		Yes
Unsworth and Engle (2005)	Explicit	Span task	Online	Sequence-specific	Yes
				Mixed	Yes
	Implicit	Span task	Online	Sequence-specific	No
				Mixed	No
Bo et al. (2009)	Explicit	Change detection	Online	Sequence-specific	Yes
Kaufman et al. (2010)	Implicit	Span task	Online	Sequence-specific	No
Bo et al. (2011a)	Implicit	Span task	Online	Mixed	No
				Sequence-specific	No
		Change detection		Mixed	Yes
				Sequence-specific	No
Weitz et al. (2011)	Explicit	Span task	Online	Sequence-specific	Yes
	Implicit				No
Bo et al. (2012)	Explicit	Change detection	Online	Sequence-specific	No
				Mixed	Yes

Engle, 2005). Frensch and Miner (1994, Experiment 1), as well as Bo and colleagues (Bo et al., 2009; Bo et al., 2012), found significant correlation between WM and some measures of explicit sequence learning. These studies suggest that WM is engaged in explicit learning to guide the focus of attention and cognitive control (Cowan, 1995; Jiménez, 2003; Kaufman et al., 2010). This idea is also supported by the more attention demanding dual-task experiments (Frensch and Miner, 1994, Experiment 2) in which sequence learning performance under dual-task conditions correlated with Digit Span and Location Span Tasks. In line with this argument, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies of sequence learning found greater activity in prefrontal cortical areas during explicit sequence learning compared to the implicit condition (Destrebecqz et al., 2005; Fletcher et al., 2005; Honda et al., 1998). Prefrontal cortical areas are thought to be engaged in WM performance as well (Champod and Petrides, 2010; Smith and Jonides, 1999).

2.2. *Measures of WM*

As the above mentioned studies have shown, different methods could lead to different WM effects on sequence learning. Performance on short-term and WM *span tasks* (e.g., Forward and Backward Digit Span, Operation Span, Reading Span, and Listening Span Tasks) shows no correlation with implicit/incidental sequence learning, while *dual-task* methods (Frensch and Miner, 1994) and *change detection* WM *tasks* (Bo et al., 2011a) can demonstrate WM effects on implicit sequence learning. In contrast, most studies have found WM effects on explicit sequence learning using any type of WM measure (e.g., Unsworth and Engle, 2005; Bo et al., 2009; Weitz et al., 2011). In addition, we also have to consider the difference between verbal and visuospatial WM depending on whether verbal (e.g., letters, digits, words) or visuospatial material (e.g., shapes, colors, locations) needs to be remembered. These two types of WM can relate to sequence learning in different ways, suggesting some extent of domain-specificity. One can assume that the performance in a sequence learning task, where the sequence is defined as a stimulus-series of different locations (e.g., classical SRT task, Nissen and Bullemer, 1987), might correlate stronger with visuospatial than with verbal WM capacity. For example, in the study of Frensch and Miner (1994, Experiment 1), visuospatial sequence learning correlated with Location Span but not with Digit Span. Similarly, Bo et al. (2009) found a relationship between sequence learning, measured by the chunk length of a visuospatial sequence learned by the participants, and visuospatial WM capacity. In contrast, verbal WM might play a greater role in sequence learning of verbal material (e.g., Dennis et al., 2006; Weitz et al., 2011). For example, a recent study by Weitz et al. (2011) showed correlation between the learning of a verbal sequence (Hebb digits task) and verbal WM capacity. Note, however, that all of these latter findings regarding domain-specificity were related to explicit and not to implicit sequence learning.

2.3. *Stages of sequence learning*

The differentiation between *online* and *offline phases of learning* also needs to be considered, as significant changes in the acquisition do not occur only during practice (online periods) but also between practice (offline) periods. The process that occurs during the offline periods is referred to as consolidation, which means stabilization of a memory trace after the initial acquisition; it can result in increased resistance to interference or even improvement in performance following an offline period (Krakauer and Shadmehr, 2006; Nemeth et al., 2010b; Nemeth and Janacsek, 2011; Robertson, 2009; Song, 2009). The previously discussed studies measured sequence learning by one learning session without an offline period and barely showed WM's effect on sequence learning. On the other hand, if we administer multiple learning sessions with, for example, 24-h delay periods, we are able to examine the effect of consolidation processes on the relationship between sequence learning and WM capacity. For example, Howard and Howard (1997) as well as Schwartz et al. (2003) administered more learning sessions distributed throughout several days and found significant WM effects on a sequence learning task. However, they did not analyze the effect of consolidation specifically (the performance from all learning sessions were collapsed). Future studies need to test the relationship between sequence knowledge after a consolidation period and WM capacity.

2.4. *General skill versus sequence-specific learning*

There seem to be a number of misunderstandings regarding the sequence learning indices used in the studies focusing on the association between sequence learning and WM. Recent studies highlight that at least two aspects of learning have to be differentiated in the sequence learning experiments. The reaction time (RT) performance improvement as a result of practice can be attributed both to general familiarization with the task (termed as *general skill learning*, or *general practice effects*) and to learning the sequential structure/regularity of the task specifically (termed as *sequence-specific learning*) (Janacsek and Nemeth, 2012; Song et al., 2007). In the classical SRT task (Nissen and Bullemer, 1987), the more the participants practice, the faster they are on blocks containing the repeated sequential structure. When this sequence is changed to a random series of stimuli at the end of practice, participants' response rate becomes slower. In this task, sequence learning can be measured in different ways: 1) by the RT decrease in sequential blocks (i.e., participants are generally faster in the last sequence block compared to the first sequence block; e.g., Bo et al., 2011a); 2) by the RT difference between the last sequence block and the subsequent random block. The latter measure is more widely accepted in sequence learning literature (e.g., Keele et al., 2003; Robertson, 2007; for critical view see Reed and Johnson, 1994). For example, using these indices, Bo et al. (2011a) found a positive correlation between WM capacity and the rate of RT decrease (thus, the RT change in sequential blocks), but not between WM and RT difference in the last sequence and the following random block (which is supposed to reflect sequence-specific learning better). In a more recent study, Bo and colleagues replicated these results in elderly participants. One potential concern regarding these results is whether it is possible to separate the above mentioned general skill and sequence-specific learning components in the classical SRT task. Namely, the RT decrease in the sequential blocks can reflect both general skill and sequence-specific learning. The contribution of these two factors to performance improvement cannot be precisely determined. As Bo et al. (2011a, 2012) found correlation only with the RT decrease in sequence blocks, not with the sequence/random difference score, we can suggest that WM might be more related to general skill learning than to the sequence-specific learning. Therefore, further studies and different analysis methods are needed to clarify the relationship between WM and general skill learning or sequence-specific learning. For example, as Verwey (1996) proposed, participants respond to individual sequence elements one by one at the beginning of the sequence learning, but consecutive elements can be formed into a single representation ("chunk") once the sequence is learned. Thus, it is possible to determine the mean chunk length in the SRT task with higher length (larger window into the sequence structure) reflecting better sequence-specific learning. Using this analysis method, Bo et al. (2009) found a relationship between WM capacity and mean chunk length in *explicit* sequence learning. This raises the question of whether such a relationship is present between the mean chunk length in *implicit* sequence learning and WM.

Another possible approach for future studies can be the use of *probabilistic* sequences instead of deterministic ones (as in the SRT task), since probabilistic second- or higher-order sequence regularities give us the opportunity to analyze sequence-specific and general skill learning separately and more precisely. For example, in the alternating SRT (Howard and Howard, 1997) task, repeating stimuli alternate with random ones, thus every second element in the stream is determined randomly. Hence, it is possible to *track sequence-specific learning continuously* by comparing responses to the random and sequence elements in all blocks. This could help to investigate the relationship between sequence-specific learning and WM more precisely.

3. Neurocognitive background of the relationship between WM and sequence learning

A growing body of evidence suggests that the fronto-striatal circuit, including the caudate nucleus and lateral PFC, plays a critical role in WM performance. In this circuit, PFC is thought to be responsible for the coordination of encoding, maintenance, and manipulation of information, by, for example, biasing the processing in posterior sensory-and multimodal association areas (Bar, 2003; Desimone and Duncan, 1995; Miller and Cohen, 2001; Nobre, 2001). The striatum, on the other hand, modulates the WM performance by increasing or decreasing the inhibition of the PFC (Ashby et al., 2010). Recent studies highlight that the striatum is primarily involved in the manipulation processes, for example filtering out the irrelevant information (McNab and Klingberg, 2007), conflict monitoring (Beste et al., 2012), and sequencing (Riley et al., 2011).

In this fronto-striatal circuit, the last two decades of implicit sequence learning research showed the involvement of striatum in the acquisition of sequence knowledge (Keele et al., 2003; Rieckmann et al., 2010), while the role of PFC remained inconclusive. Determining the specific conditions where WM capacity and sequence learning correlate can help us to unravel the complex role of PFC in cognition and specifically in sequence learning. In most studies finding correlation between these two measures, participants were aware of the sequence and had the intention to improve their performance utilizing this sequence knowledge. In these cases a higher extent of PFC-dependent coordination and cognitive control is implemented to perform the task. Supporting this argument, fMRI studies found greater PFC activation in this explicit/intentional version of sequence learning compared to the implicit/incidental one (e.g., Fletcher et al., 2005). Thus, the relationship between WM capacity and sequence learning in these cases might be based on the mutual PFC-dependent coordination component of the performance.

However, in some cases implicit sequence learning was also correlated with WM capacity. In most of these studies WM capacity was measured by a complex task where the manipulation of the information, not only the maintenance, was relevant for a high task performance. Based on these results we can suggest that this observed correlation is primarily attributable to the greater involvement of the striatum in these WM tasks. The recent studies showing the specific role of striatum in information manipulation are in line with this assumption (Beste et al., 2012; Riley et al., 2011). The other plausible explanation could be that most of the studies finding a relationship administered more sessions to measure sequence learning (Howard and Howard, 1997; Schwartz et al., 2003), allowing a better consolidation of the acquired information. One might assume that processes engaged in this offline phase of sequence learning share more similarity with WM than the online sequence processing (e.g., maintaining the acquired information in an active state for a longer period can help stabilize the memory traces). However, these studies did not contrast the online and offline performance directly and did not involve brain imaging; therefore future research needs to clarify this issue.

4. Summary

In our review, we briefly touched on some relevant issues regarding the possible relationship between implicit sequence learning and WM: 1) the explicitness of the sequence; 2) measures of WM capacity; 3) online and offline stages of sequence learning; and 4) general skill- and sequence-specific learning. With these factors we can better interpret the results of studies on the relationship between sequence learning and WM. However, note that because of the length limitation of the mini-review we could not critically investigate the question of whether the implicit sequence learning and WM tasks discussed in this mini-review are the most adequate measures for tapping the constructs they were designed to tap (Kane et al., 2007; Moisello et al., 2009; Unsworth and Engle, 2006).

Based on the studies included in this mini-review (Table 1), we suggest a relationship between WM and 1) explicit rather than implicit sequence learning, 2) potentially to a higher extent with general skill learning than with sequence-specific learning, 3) with some specificity to verbal or visuospatial domains (i.e., higher correlation between visuospatial WM and learning of visuospatial sequences than learning verbal ones). In the reviewed literature only two studies have administered multiple sessions to measure sequence learning. However, they analyzed the relationship between WM and sequence learning by collapsing the online and offline components. Therefore, the effect of consolidation on this relationship remains an open question needing to be addressed in further research. In addition, future studies also would benefit from taking into account which measures are used for determining the WM capacity (i.e., span or change detection tasks) as well as sequence learning (i.e., general RT improvements, RT difference between sequence and random elements, chunk length of the sequence, etc.).

Considering the factors discussed in this mini-review will aid in the design of future experiments, in the interpretation of results, and a deeper appreciation of the relationship between sequence learning and WM and underlying brain structures.

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