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Enhancing the neuroplasticity of statistical learning through brain stimulation and behavioral interventions

PhD Thesis

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List of publications related to this thesis

I. **Szücs-Bencze, L.,** Vékony, T., Pesthy, O., Kocsis, K., Kincses, T. Zs., Szabó, N., & Nemeth, D., (2025). Enhancing retrieval capacity of the predictive brain through dorsolateral prefrontal cortex intervention. *Cerebral Cortex, 35*(2).
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List of abbreviations

AIC = Akaike Information Criterion

ANOVA = one-way analysis of variance

ASRT = Alternating Serial Reaction Time

cTBS = continuous theta burst stimulation

DLPFC = dorsolateral prefrontal cortex

fMRI = functional magnetic resonance imaging

iTBS = intermittent theta burst stimulation

M1 = primary motor cortex

PALT = Paired-Associate Learning Task

PFC = prefrontal cortex

RT = reaction time

rTMS = repetitive transcranial magnetic stimulation

SL = statistical learning

SRT = Serial Reaction Time

TBS = theta burst stimulation

TMS = transcranial magnetic stimulation

TP = transitional probability

VSL = visual statistical learning

Introduction

The human brain's powerful ability to constantly pick up patterns and regularities in the environment is known as statistical learning (SL). This broad mechanism enables individuals to extract probabilistic structures from sensory input (Schapiro, Kustner & Turk-Browne, 2012), shaping perception, cognition, and behavior. At its core, SL involves tracking the frequency and co-occurrence of elements over time to predict future events. A key concept in this process is transitional probabilities (TPs)—the likelihood that one element (such as a sound, visual shape, or movement) will be followed by another based on past patterns (Saffran, Newport & Aslin, 1996). Recent definitions further emphasize key attributes of SL, such as its implicit nature (operating without conscious awareness) and its incidental nature (occurring effortlessly in everyday life) (Obeid, Brooks, Powers, Gillespie-Lynch & Lum, 2016; Arciuli, 2017).

Throughout the course of our lives and across various domains, we engage in SL without being consciously aware of it. A well-known example comes from language learning: infants as young as eight months old can pick up word boundaries in continuous speech by detecting TPs between syllables (e.g., *ba* and *by* in "baby") rather than between words (Saffran, Aslin & Newport, 1996). Beyond language, SL also underlies motor skill acquisition—for instance, when learning a new sport or musical instrument, individuals unconsciously recognize recurring movement sequences, allowing for smoother and more efficient performance over time (Hunt & Aslin, 2001). Social skills also require the involvement of SL. People naturally track patterns in others' behaviors, such as facial expressions, gestures, or tone of voice, to predict emotions and social intentions (Parks, Griffith, Armstrong & Stevenson, 2020). This helps us navigate social interactions smoothly, for example, by anticipating how someone might react in a conversation. SL has also been linked to higher-level cognitive processes, such as reasoning and decision-making. Studies suggest that individuals who are better at detecting statistical regularities also perform better on tasks requiring cognitive flexibility and problem-solving, as they can more efficiently extract relevant patterns from their environment (Sherman, Graves & Turk-Browne, 2020).

Acquiring various cognitive and motor skills enables us to navigate the world efficiently. However, several medical conditions can impair these skills. In Parkinson's disease, patients often experience impairments in language or visuospatial skills (Papagno & Trojano, 2018).

Similarly, stroke survivors often experience motor deficits, particularly in fine motor skills, which hinder daily activities (Wessel, Zimerman & Hummel, 2015). Furthermore, individuals with spatial neglect—a condition affecting spatial awareness post-stroke—may struggle with representational updating, a process reliant on SL. Targeted interventions that promote SL could improve their ability to adapt to changing environments (Shaqiri, Anderson & Danckert, 2013). Given that SL is fundamental to acquiring and refining cognitive and motor skills, developing interventions to enhance this learning process is crucial in rehabilitation. In this thesis, I will present two studies that explore how different phases of SL—specifically consolidation (how learned patterns are stabilized and stored) and retrieval (how stored knowledge is accessed and applied)—can be modulated through brain stimulation and behavioral interventions. The first study investigates how transcranial magnetic stimulation (TMS) of the dorsolateral prefrontal cortex (DLPFC) influences the retrieval of learned statistical patterns. The second study examines how manipulating the temporal structure of the learning process—specifically, the duration of breaks between learning blocks—affects the consolidation of statistical knowledge. By investigating these approaches, these studies aim to provide insights into effective strategies for enhancing SL in healthy individuals, which can later be applied to clinical populations as well.

Statistical learning in contemporary cognitive frameworks

SL is now understood as a fundamental cognitive process that allows individuals to extract regularities from their environment (Frost, Armstrong, Siegelman & Christiansen, 2015). However, its precise relationship with broader cognitive systems—particularly implicit learning, procedural memory, and the habitual system—has been an area of active debate.

Firstly, SL is often classified as a type of implicit learning—a form of learning that occurs without conscious intention or awareness (Reber, 1967). Although both implicit learning and SL refer to an incidental learning mechanism, SL is thought to operate through statistical computations, whereas implicit learning is suggested to rely on chunk formations (Perruchet & Pacton, 2006). Additionally, SL has been linked to procedural memory—a component of long-term memory responsible for learning skills and habits (Ullman, 2004). SL and procedural memory both rely on gradual, experience-dependent learning and involve automatized processes that improve with practice. However, SL is not exclusively motor-based, while procedural memory is often tied to motor and cognitive skill acquisition. Finally, SL is also thought to involve the habitual system, which refers to automatic, stimulus-driven behaviors that are reinforced through repeated exposure (Ashby & Crossley, 2012). This notion is supported by studies showing that divided attention does not disrupt SL, indicating that the acquired regularities can indeed become habitual and automatic (Horváth, Török, Pesthy, Nemeth & Janacsek, 2020; Nemeth et al., 2011).

To sum up, SL can be seen as a subtype of implicit learning, operating without conscious awareness to extract probabilistic regularities. It shares characteristics with procedural memory, particularly in its gradual, experience-driven nature, but it is not exclusively motor-based. Last but not least, it is linked most strongly to the habitual system, as repeated exposure to statistical regularities can lead to automaticity in behavioral responses.

The rise of non-linguistic statistical learning

Initially conceptualized within the framework of implicit learning (Reber, 1967), SL became widely recognized in linguistic research during the 1990s. Pioneering studies provided evidence that infants could extract regularities from speech without explicit instruction (Saffran et al., 1996a). Following this discovery, researchers explored the role of SL in various linguistic domains (e.g., phonotactic learning and syntactic structure acquisition). While initial research on SL was predominantly language-focused, as evidence accumulated, it became clear that SL extends beyond language, influencing perception, motor learning, and cognitive processing. Accordingly, research in the 2000s began expanding beyond linguistic contexts in exploring how SL operates across multiple sensory modalities, including auditory, visual, and motor systems. For example, early studies of high importance have demonstrated that adults and infants could extract regularities from visual scenes, suggesting that SL is not limited to language but also applies to visual perception and revealing the concept of visual statistical learning (VSL) (Fiser & Aslin, 2001, 2002). Another cornerstone in SL research was the introduction of the Serial Reaction Time (SRT) task (Nissen & Bullemer, 1987), along with its more advanced versions, such as the Alternating Serial Reaction Time (ASRT) task (Howard & Howard, 1997, 2004), which enable the measurement of SL within the visuomotor domain.

Due to the development of non-linguistic paradigms, it has been suggested that SL is a fundamental, domain-general cognitive ability, meaning that the brain applies similar learning principles across different perceptual and cognitive domains (Conway & Christiansen, 2005).

The latest frameworks, however, debate whether SL functions as a single, fully unified mechanism, proposing instead that it operates as a collection of domain-general principles with specific characteristics that may vary across different modalities (Frost et al., 2015; Siegelman, Bogaerts & Frost, 2018).

Measuring statistical learning in the visuomotor domain

The emergence of sequence learning tasks has significantly advanced our ability to study SL mechanisms, particularly in scenarios where multiple modalities (e.g., visual and motor) work in concert (Pedraza, Vékony & Nemeth, 2023). The SRT task is a four-choice reaction time task that typically involves presenting participants with visual stimuli on a screen, where they are required to respond as fast as possible to these stimuli using motor actions, such as pressing a button (Nissen & Bullemer, 1987). Participants are usually not informed that the sequence of visual stimuli follows a regular pattern. In the SRT task, learning is typically inferred by comparing reaction times (RTs) for sequence-based trials and randomly inserted trials. When a random sequence is introduced, RTs tend to slow down, indicating a disruption in learned patterns. This task has been widely used to investigate implicit learning processes, including the acquisition of non-conscious statistical regularities, such as TPs between successive stimuli, particularly in the domain of motor skills.

The SRT task has been a cornerstone in studying implicit learning, but it also has notable limitations. One key drawback is that learning can only be assessed intermittently by inserting blocks of random stimuli. Another limitation stems from the deterministic nature of the sequence used in the traditional SRT task. In most versions, the task relies on first-order conditional sequences, meaning that each element in the sequence can be predicted with 100% certainty based on the preceding one (Robertson, 2007). This deterministic structure increases the likelihood that participants will consciously recognize the pattern, shifting the task from measuring implicit SL to capturing explicit learning processes. Consequently, the SRT task may not provide a pure measure of SL, as participants might rely on explicit memory rather than unconsciously extracting regularities from the environment, which is, as previously discussed, a key attribute of SL.

In response to these limitations, more advanced versions of the SRT task, such as the ASRT task, were introduced. The ASRT task (Howard & Howard, 1997; Howard et al., 2004) builds on the SRT task by incorporating a probabilistic sequence structure in which pattern and random elements alternate, giving rise to its name (Howard & Howard, 1997). Due to this probabilistic sequence structure, some stimuli appear with higher probability than others (Janacsek, Fiser & Nemeth, 2012). Participants, without explicit awareness, become sensitive to the second-order statistical regularities, responding faster to high-probability stimuli (Janacsek et al., 2012). This design offers several advantages that make it particularly useful for studying SL. One key advantage of the ASRT task is its strong reliability: test-retest reliability is higher than in the traditional SRT task (Stark-Inbar, Raza, Taylor & Ivry, 2016), and its internal consistency is also well-supported (Farkas, Krajcsi, Janacsek & Nemeth, 2023). A second advantage is that, unlike the SRT task, the ASRT design allows for continuous assessment of the learning process without the need to interrupt it with inserted random sequences. This is particularly important when investigating different phases of learning, such as consolidation and retrieval. The third advantage lies in the probabilistic nature of the sequence itself, where the pattern is embedded within noise. This makes it less likely that participants will become explicitly aware of the sequence, preserving the implicit nature of SL (Howard et al., 2004; Song, Howard & Howard, 2007). Finally, the ASRT task, unlike its deterministic counterpart, allows researchers to distinguish between distinct learning processes, such as general skill learning and SL (Szegedi-Hallgató, Janacsek & Nemeth, 2019). General skill learning refers to the overall RT improvement throughout task performance that occurs as a result of practice. On the other hand, SL refers to the implicit acquisition of regularities within the task structure.

As presented in the section *The rise of non-linguistic statistical learning*, SL is a general learning mechanism that can be measured across various modalities. Since the studies discussed in this dissertation focused on implicit SL in the visuomotor domain, the following sections will specifically review research examining the learning dynamics, neural background, and modulation of SL within this domain, while findings from other modalities will only be mentioned briefly when relevant.

The dynamics of statistical learning: From acquisition to retrieval

Learning is the process by which individuals acquire knowledge or skills through repeated exposure, practice, or experience. However, the development of knowledge is not confined to the period of active learning; it can continue to evolve between sessions, either during wakefulness or sleep. The progress of SL can be examined through behavioral measures such as RTs or accuracy, which indicate how learning unfolds over time (Howard et al., 2004; Nemeth, Janacsek & Fiser, 2013).

The acquisition phase marks the initial stage of learning, where individuals begin to detect and respond to patterns in a sequence. Research suggests that probability-based SL occurs rapidly, with the participants demonstrating sensitivity to statistical patterns within the very first block of trials (Simor et al., 2019). This indicates that even minimal exposure—only a few repetitions of a pattern—is sufficient for learning to take place (Kóbor et al., 2018; Szegedi-Hallgató et al., 2017). However, additional practice strengthens this statistical knowledge, suggesting that learning continues to be refined over time (Simor et al., 2019). Since SL is evident after a single training session, this type of learning is indicated to be a fundamental mechanism by which individuals automatically adapt to environmental regularities (Song et al., 2007; Nemeth et al., 2013a; Kóbor et al., 2018). Although SL predominantly occurs without conscious awareness, some researchers argue that attention to stimuli may play a role in the effectiveness of SL (Toro, Sinnett & Soto-Faraco, 2005; Turk-Browne, Jungé & Scholl, 2005). Nevertheless, findings indicate that SL can persist over long periods, even with brief exposure (Kim, Seitz, Feenstra & Shams, 2009).

Once SL occurs, consolidation stabilizes and strengthens the acquired knowledge, allowing it to be retained over time. Although some studies suggest that auditory SL may benefit from sleep (Durrant, Cairney & Lewis, 2013; Durrant, Taylor, Cairney & Lewis, 2011), evidence within the visuomotor domain remains scarce. Studies investigating the consolidation of probabilistic sequence learning (i.e., measured by the ASRT task) suggest that, unlike deterministic sequences (i.e., measured by the SRT task) (King, Hoedlmoser, Hirschauer, Dolfen & Albouy, 2017; Robertson, Pascual-Leone & Press, 2004), learning probabilistic patterns does not seem to benefit from post-learning sleep in terms of behavioral performance (Song et al., 2007; Nemeth et al., 2010). One study reported that SL remained intact regardless of whether participants remained awake, rested quietly, or slept after learning (Simor et al., 2019). This finding aligns with prior research showing no clear sleep-related consolidation effects for probabilistic sequence learning tasks (Peigneux et al., 2003, 2006; Song et al., 2007; Nemeth et al., 2010). A new avenue of consolidation research is rapid consolidation, which involves the stabilization and enhancement of just-learned statistical knowledge during short offline rest periods (Bönstrup et al., 2019). Studies investigating the role of such rapid consolidation in SL have found that SL occurs exclusively online and does not benefit from short offline rest periods (Fanuel et al., 2022; Quentin et al., 2021).

Retrieval refers to the ability to access and utilize previously learned information. Although studies specifically focusing on the retrieval phase in visuomotor SL are limited, evidence suggests that once statistical knowledge is consolidated, it can be accessed and utilized even after extended delays (Kóbor, Janacsek, Takács & Nemeth, 2017; Tóth-Fáber, Nemeth & Janacsek, 2023). Previous findings have demonstrated stable retention of statistical knowledge across various time intervals, ranging from several hours to one year (Kóbor et al., 2017; Nemeth & Janacsek, 2011; Meier & Cock, 2014). The resilience of SL over time suggests that the acquired knowledge remains well-preserved, showing resistance to forgetting and interference (Kóbor et al., 2017). These results align with everyday experiences, such as maintaining skills in language or motor activities, which persist long after they are first learned (Kóbor et al., 2017).

Overall, the dynamic nature of SL involves a rapid acquisition phase, a consolidation phase where knowledge remains stable over time, and a retrieval phase where learned statistical patterns can be accessed and applied even after long delays. These findings highlight the robustness of SL, raising the question of how this resilient mechanism can be influenced through behavioral and brain stimulation interventions.

Neural background of statistical learning

Early research primarily attributed SL to sensory-specific brain regions. According to this view, SL is computed within the sensory areas associated with specific modalities (Frost et al., 2015). In VSL, for example, the occipital cortex and inferior temporal cortex are primarily engaged (Turk-Browne, Scholl, Chun & Johnson, 2009). Motor-based SL, on the other hand, involves interactions between the primary motor cortex (M1) and the premotor cortex (Wymbs et al., 2012). However, statistical regularities do not solely activate modality-specific sensory regions; they also recruit broader cortical structures. The left inferior frontal gyrus, for instance, has been implicated in processing statistical patterns not only in speech (Karuza et al., 2013) but also in visual stimuli (Turk-Browne et al., 2009). This suggests that SL involves both domain-specific and domain-general mechanisms.

While SL relies on a widespread cortical network, subcortical structures—including the hippocampus, basal ganglia, and cerebellum—are also critically involved. The basal ganglia play a fundamental role in the procedural, non-declarative memory system (Ullman, 2004), whose connection to SL has already been outlined in the section on *Statistical learning in contemporary cognitive frameworks*. Basal ganglia are shown to be responsible for extracting predictable patterns through repeated exposure (Berns, McClure, Pagnoni & Montague, 2001). Evidence from neuropsychological studies supports this role: individuals with Parkinson's disease, which affects basal ganglia function, exhibit deficits in SL (Wilkinson, Khan & Jahanshahi, 2009). Furthermore, the hippocampus and medial temporal lobe, traditionally associated with declarative memory (Squire, 2004), also contribute to SL. The hippocampus is particularly involved in extracting temporal relationships between sequence elements (Schapiro, Gregory, Landau, McCloskey & Turk-Browne, 2014) and facilitating pattern integration over time, which aids in generalization (Schuck & Niv, 2019). Empirical findings further highlight its role since fMRI studies reveal hippocampal activation during VSL (Schapiro et al., 2012).

Importantly, a growing body of research suggests that SL relies on interaction between multiple cognitive systems and diffuse neural networks rather than a single unified process and separate brain regions (Schapiro, Turk-Browne & Botvinick, 2017). The prefrontal cortex (PFC) seems to play a crucial role in the top-down regulation of SL-associated subcortical structures. Firstly, the frontostriatal network, which links the PFC and basal ganglia, plays a key role in balancing habitual and goal-directed learning mechanisms (Doyon et al., 2009; Naismith et al., 2010; Janacsek et al., 2012, 2020). However, a PET study found that the interaction between the PFC and basal ganglia may depend on the intentionality of learning: during implicit learning, the caudate nucleus exhibits significantly higher activity, which is decoupled from the activity of the PFC. In contrast, when participants acquire explicit knowledge, the PFC becomes more active, exerting control over the striatum (Destrebecqz & Cleeremans, 2005). This finding is in line with those fMRI studies that found that reduced PFC engagement favors implicit SL performance (Park, Janacsek, Nemeth & Jeon, 2022; Tóth et al., 2017).

The hippocampus also interacts with both the prefrontal and striatal systems to support the encoding and consolidation processes of auditory and visual regularities (Henin et al., 2021). A diffusion tensor imaging study revealed that probabilistic SL is associated with the integrity of the tracts connecting the caudate nucleus to the DLPFC and the hippocampus to the DLPFC

(Bennett, Madden, Vaidya, Howard & Howard, 2011). Moreover, the PFC exerts inhibitory control over hippocampal activity, which influences memory functions, including retrieval (Benoit, Hulbert, Huddleston & Anderson, 2015; Woodcock, White & Diwadkar, 2015; Oehrn et al., 2018). The dual-process perspective further posits that SL arises from a combination of bottom-up statistical computations and top-down cognitive control mechanisms (Conway, 2020).

The neural substrates of SL involve an intricate, dynamic network of cortical and subcortical structures, highlighting the integration of various learning and memory systems in the extraction and application of statistical regularities. Establishing a unified cognitive model of SL, along with such a diffuse neural network, is a major challenge.

Modulating statistical learning through non-invasive brain stimulation

TMS is a type of non-invasive brain stimulation (NIBS) that modulates neural activity by delivering magnetic pulses to targeted brain regions. By placing a coil against the scalp, TMS generates magnetic fields that induce electrical currents in the underlying cortical tissue, thereby influencing neuronal communication and excitability. TMS is a powerful tool for studying cognitive functions because it allows researchers to casually manipulate neural activity in specific brain regions, providing insights into their role in learning and memory while maintaining high temporal precision (Bergmann & Hartwigsen, 2021; Pascual-Leone, Gates & Dhuna, 1991). The latter property is particularly important when studying different phases of learning mechanisms.

The effect of TMS on SL depends on several factors. A review study identified six key factors that influence the behavioral effects of TMS: TMS protocol, targeted brain area and hemisphere, timing of the stimulation, complexity of the sequence, and methodological details (Szücs-Bencze et al., 2023). Regarding the protocol, repetitive TMS (rTMS) is performed by repeatedly applying magnetic pulses, which can have either facilitatory or inhibitory effects on the cortex, depending on the frequency of the delivered pulses (Huang et al., 2017; Polanía, Nitsche & Ruff, 2018). Typically, high-frequency rTMS is thought to have a facilitatory effect, while low-frequency rTMS is considered to be inhibitory. The patterned form of TMS, known as theta burst stimulation (TBS), also has faciliatory and inhibitory protocols depending on whether the pulse bursts are delivered intermittently (iTBS) or continuously (cTBS) (Huang, Edwards, Rounis, Bhatia & Rothwell et al., 2005). The TMS protocols can interact with the role of a specific brain area. The activity of the targeted brain area can either support or counteract the function of a specific cognitive process; thus, even with an inhibitory protocol, a facilitatory effect can still be achieved (Ambrus et al., 2020; Smalle, Daikoku, Szmalec, Duyck & Möttönen, 2022). Additional factors include which hemisphere is being stimulated: hemispheric lateralization can be explored (Galea, Albert, Ditye & Miall, 2010), or bilateral stimulation can maximize TMS effects by preventing compensatory mechanisms of the hemispheres (Andoh & Martinot, 2008). Timing is also a crucial factor in determining the effects, as the phase of the learning process (acquisition, consolidation, or retrieval) during which the stimulation is applied influences the outcome (Veldman et al., 2018). The complexity of the sequence is another important consideration, as different brain areas may be involved in simpler deterministic versus more complex probabilistic sequences (Clark et al., 2019). Furthermore, methodological details, such as the control group used (e.g., active control or sham) and the determination of stimulation intensity, can be critical in shaping the effects of TMS on SL.

The impact of TMS during the initial learning phase has been examined in several studies. TMS can be administered either simultaneously with task performance or between learning blocks. For example, facilitatory TMS over the DLPFC administered during sequence learning on the SRT task led to a decline in task performance (Pascual-Leone, Wassermann, Grafman & Hallett, 1996). In contrast, a more recent study found that inhibitory TMS over the DLPFC applied between learning blocks resulted in improved performance on the ASRT task (Ambrus et al., 2020). The majority of research, however, has focused on so-called ‘off-line stimulation’, where TMS is delivered before the task, with most studies reporting impaired learning of SL (Clark et al., 2019; Clerget, Poncin, Fadiga & Olivier., 2012; Wilkinson et al., 2015).

Beyond the learning phase, TMS has also been applied to investigate its influence on the consolidation of statistical knowledge. For example, continuous theta burst stimulation (cTBS)—a patterned form of TMS—over the DLPFC has been shown to enhance performance on a deterministic sequence after an eight-hour offline period (Galea et al., 2010). Conversely, studies applying inhibitory TMS over the M1 have found that it interferes with offline improvement in implicit SL during the day (Robertson, Press & Pascual-Leone, 2005), as well as in explicit learning after sleep (Breton & Robertson, 2017). These findings suggest that rTMS over both the DLPFC and M1 can significantly influence the consolidation of memory traces by modulating the processes underlying memory stabilization.

Despite substantial research on the effects of TMS during the learning and consolidation phases, little attention has been paid to its potential role in the retrieval phase of SL. To date, no studies have investigated the impact of TMS immediately before or during the access of well-acquired statistical knowledge. Given the lack of evidence in this area, one of the primary aims of the current thesis is to fill this gap and present my own results on the TMS effects as applied over the DLPFC on SL retrieval.

Modulating statistical learning through behavioral approaches

Applying various behavioral interventions in SL can help us understand the different phases of this fundamental and complex mechanism. Which behavioral methods can be used to test the acquisition phase of SL? The impact of instructions on SL has been explored using the ASRT task. Vékony, Pleche, Pesthy, Janacsek and Nemeth (2022) examined whether prioritizing speed or accuracy during learning influenced different aspects of SL. Their results indicated that emphasizing speed enhanced probability-based learning. However, after a retention period where participants focused equally on speed and accuracy, both groups demonstrated comparable acquired knowledge. Stress is another crucial factor in learning and memory. Tóth-Fáber, Janacsek, Szőllősi, Kéri and Nemeth (2021) investigated its effects on different aspects of SL using the ASRT task. Contrary to intuition, results demonstrated that acute stress, far from impairing, actually enhanced the acquisition of probability-based regularities in the early learning phase. The role of attention in SL, on the other hand, remains a topic of debate. Horváth and colleagues (2020) explored whether dividing attention during learning affects the acquisition of statistical regularities. Results indicated that divided attention had no effect on the acquisition of probabilistic sequences. These findings suggest that SL is robust to attentional manipulations, reinforcing the idea that minimal attentional resources are required for learning statistical regularities. This notion is further supported by the findings of Nemeth, Janacsek, Polner and Kovacs (2013), who compared SL in a hypnotic state to an alert state. Their results indicated that hypnosis facilitated the acquisition of non-adjacent regularities. These findings highlight that the cognitive control-dependent system is not necessary for effective SL. In fact, its disengagement may be beneficial for learning. These insights provide valuable implications for optimizing strategies in various settings.

The consolidation of SL is influenced by multiple factors, including awareness, attentional conditions, and the nature of the learned sequence (Janacsek & Nemeth, 2012). Regarding awareness, it has been proposed that the consolidation of explicit and implicit learning follows distinct pathways (Robertson, 2009). Findings suggest that sleep-dependent consolidation occurs only when participants possess explicit sequence knowledge (Fischer, Hallschmid, Elsner & Born, 2002; Robertson et al., 2009; Walker & Stickgold, 2004). In contrast, implicit SL consolidation appears to be time-dependent rather than sleep-dependent. Furthermore, sleep benefits simple, explicit sequence structures but does not enhance the consolidation of complex, probabilistic sequences (Nemeth et al., 2010; Robertson et al., 2004; Song et al., 2007). Thus, awareness and sequence structure modulate the role of sleep in consolidation. Horváth and colleagues (2020) demonstrated that statistical knowledge remains preserved even when acquired under divided attention, suggesting that the consolidation process of implicit SL is as robust as acquisition. Most consolidation studies have examined time frames spanning hours. However, recent research has begun investigating rapid consolidation, which occurs within seconds (Bönstrup et al., 2019). Previous findings indicated that both deterministic and probabilistic sequence learning benefits from extended two-minute rest periods (Du, Prashad, Schoenbrun & Clark, 2016) and even shorter ten-second rest periods (Bönstrup et al., 2019). However, the latest studies suggest that consolidation occurs exclusively online and does not benefit from short offline periods (Fanuel et al., 2022; Quentin et al., 2021). The current thesis aims to provide a more comprehensive approach to test rapid consolidation's role in implicit visuomotor SL.

Compared to acquisition and consolidation, retrieval remains the least studied phase of SL. A study explored whether the retrieval of well-established probabilistic sequence knowledge is affected by a concurrent secondary task (Vékony et al., 2020). The findings suggest that while dual-task conditions slow response execution, they do not hinder the retrieval of learned statistical knowledge. Understanding the robustness of SL under different retrieval conditions can provide valuable insights into real-world scenarios where people must apply previously learned statistical knowledge while simultaneously managing other cognitive demands.

Aims

This thesis presents two studies that aim to address gaps in the literature related to the modulation of SL consolidation and retrieval (Table 1). While prior research has largely converged on the idea that inhibitory TMS over the DLPFC facilitates SL and its consolidation (e.g., Ambrus et al., 2020; Galea et al., 2010), no study has yet explored its effects on the retrieval of well-established statistical knowledge. To address this gap, **Study I** examined how inhibitory stimulation over the DLPFC affects the retrieval of previously acquired implicit probabilistic sequences. Participants first learned the ASRT sequence, and after a 24-hour offline period—allowing consolidation to occur—they were asked to perform the same sequence again. Before this retrieval phase, inhibitory TMS was applied over the DLPFC. A novel aspect of this study is its comprehensive investigation of hemispheric contributions to retrieval: participants were divided into separate groups receiving stimulation over the left DLPFC, right DLPFC, or both hemispheres (bilateral stimulation). To assess the effects of TMS on access to implicit statistical knowledge, the performance of the experimental groups was compared to that of a sham stimulation group, which did not receive real stimulation.

Previous research has yielded conflicting findings regarding whether rapid consolidation occurs during short rest periods introduced in SL. Some studies suggest that SL of probabilistic sequences benefits from such brief rest periods (Du et al., 2016), while others report no observable improvement (Quentin et al., 2021), and some even indicate that SL performance deteriorates during these rest periods (Fanuel et al., 2022). However, these studies either used fixed-duration rest periods or did not control for break length. Based on these inconsistencies, **Study II** investigated whether different rest period durations differentially affect SL. In this study, participants completed the ASRT task and were randomly assigned to one of three between-subject conditions regarding the length of the short rest periods: (1) 15-second breaks, (2) 30-second breaks, or (3) a self-paced condition in which they determined the duration of their own breaks. Given that the ASRT task allows for the dissociation of parallel learning processes, we examined whether rest period duration had distinct effects on SL performance (implicit acquisition of probability-based sequence structure) and general skill learning performance (reaction time improvement irrespective of the statistical probabilities). Beyond assessing overall performance, we also compared how the three groups' learning evolved both online (within learning blocks) and offline (between learning blocks) for these two distinct learning processes.

Table 1. The literature gaps and main research questions to fill them

	Literature gap to be filled		Research questions
Study I	The role of the DLPFC in the retrieval of statistical knowledge	a.	Does inhibitory TMS over the DLPFC modulate the retrieval phase of SL?
		b.	Does the effect of DLPFC inhibition on retrieval differ based on hemispheric lateralization (left, right, or bilateral stimulation)?
Study II	The role of rapid consolidation in SL	a.	How does short rest periods of different length affect SL performance?
		b.	Does rest period length influences SL differently in online (within-block) and offline (between-block) phases?

Materials and methods

Study I – Brain stimulation intervention to SL retrieval

Participants

A total of 104 healthy adult volunteers participated in this study. Two individuals were excluded due to a reported history of neurological or psychiatric disorders, and one participant did not complete the study. As a result, the final sample included 101 participants, all of whom had normal or corrected-to-normal vision and no contraindications for TMS (such as metal implants or pacemakers). At the beginning of the first session, after completing a TMS contraindication questionnaire, participants were randomly assigned to one of four groups: Left DLPFC, Right DLPFC, Bilateral DLPFC, or Sham, with no significant differences in sex, age, education, handedness, or working memory performance between groups (Table 2). Each participant provided written informed consent before taking part in the study. The study was approved by the Regional Scientific and Research Ethics Committee of the Albert Szent-Györgyi Clinical Center, University of Szeged, following the Declaration of Helsinki.

Table 2. Descriptive statistics of the four experimental groups

	Left DLPFC (n = 25)	**Right DLPFC (n = 26)**	**Bilateral DLPFC (n = 25)**	**Sham (n = 25)**
Gender (f/m)	14/11	18/8	13/12	17/8
Age (years)	23.76 ± 5.15	26.11 ± 7.26	22.40 ± 4.27	25.88 ± 6.02
Education (years)	15.40 ± 2.70	15.73 ± 2.82	14.40 ± 2.50	16.08 ± 3.53
Handedness (r/l/a)	24/1/0	23/1/2	21/4/0	21/2/2
Counting Span Task	4.41 ± 0.62	4.28 ± 0.52	3.96 ± 0.76	3.98 ± 0.76

Notes. Mean and SD values for age years of education and Counting Span Task are presented. For gender (f = female, m = male) and handedness (r = right, l = left, a = ambidextrous), case numbers are presented.

Stimuli

Implicit visuomotor SL was measured using the ASRT task. The task was implemented and executed in the E-Prime 3.0 software environment. During the ASRT task, a visual stimulus (a Dalmatian dog’s head) appeared in one of the four horizontally arranged locations on the screen. Participants were required to press the corresponding key (Z, C, B, or M on an external

QWERTY keyboard, corresponding to the four locations from left to right) as quickly and accurately as possible. Participants used their left middle and index fingers to press the Z and C keys, while their right middle and index fingers were used to press the B and M keys. The stimulus remained on the screen until a response was made, followed by a 120-millisecond (ms) response-to-stimulus interval before the next stimulus appeared. Unbeknownst to the participants, the sequence of stimuli followed a predetermined probabilistic pattern: an eight-element sequence in which pattern-defined positions alternated with randomly determined positions (e.g., 2–R–4–R–3–R–1–R, where numbers denote specific positions and "R" represents a randomly selected location). This eight-element sequence was repeated 10 times within a learning block, resulting in 80 trials per block (Fig. 1a). Due to this alternating sequence structure, certain three-element stimulus sequences (triplets) appeared with different probabilities. Trials of high-probability triplets, where the third element was more predictable based on the first element, occurred in 62.5% of trials, while trials of low-probability triplets, where the third element was less predictable, appeared in 37.5% of trials (Fig. 2b). SL was measured as the increasing RT difference between trials containing the third element of a high-probability versus a low-probability triplet.

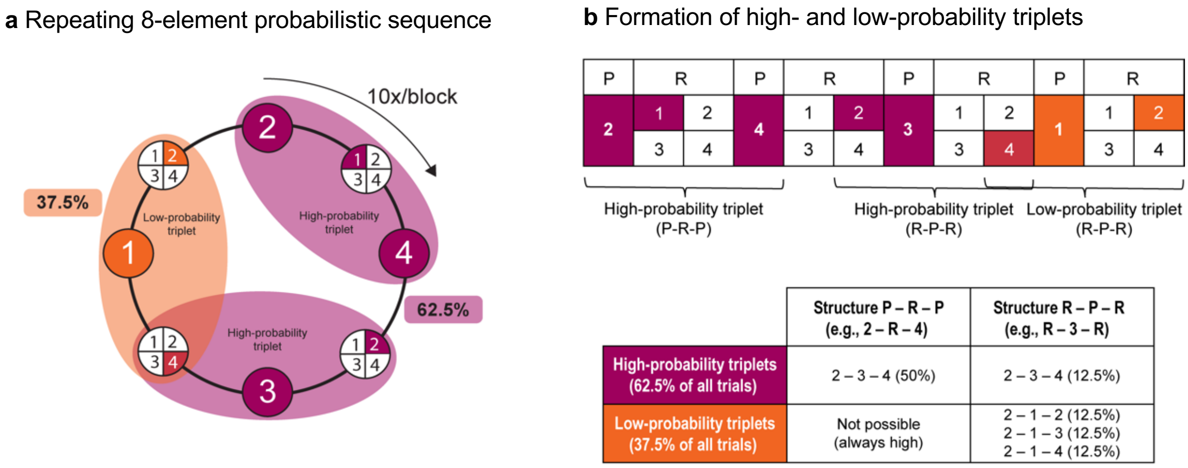

Figure 1. The ASRT task. (a) Without the participants' awareness, the visual stimuli presented in the task followed an 8-element probabilistic sequence, where pattern elements alternated with randomly inserted elements. This 8-element sequence was repeated 10 times within a learning block. (b) The probabilistic sequence structure resulted in certain three-stimulus combinations occurring more frequently (high-probability triplets) than others (low-probability triplets). Trials were classified based on whether they represented the final element of a high- or low-probability triplet. The RT difference between these trial types reflects implicit visuomotor SL.

To ensure that the effect of DLPFC stimulation was specific to SL and did not extend to explicit learning, we included a control memory task measuring declarative/episodic learning and memory. The Paired-Associate Learning Task (PALT) (Nagy, Kónya & Király, 2013) was used for this purpose and was administered via E-Prime 3.0. In the learning phase, participants were shown 23 pairs of schematic images, each containing one object and one animal, displayed side by side. Participants were instructed to name the images but were not informed that they needed to memorize them. During the retrieval session, participants were presented with 32 image pairs and had to determine whether (i) the pair had been shown in the learning phase and, if so, (ii) whether the images were presented together or rearranged. The 32 pairs were categorized into four conditions (eight pairs each): (1) Old-Old original (both images were originally paired together), (2) Old-Old rearranged (both images were from the learning phase but paired differently), (3) Old-New or New-Old (one image was from the learning phase, the other was new), and (4) New-New (neither image was shown previously). Participants' responses were recorded by the experimenter, who pressed a corresponding button (1–5) to log the answer and present the next pair. A 500 ms fixation cross was displayed between trials.

Repetitive transcranial magnetic stimulation (rTMS)

rTMS was applied using a Magstim Rapid^2 Stimulator and a D702 70 mm figure-of-eight coil (The Magstim Company Ltd, Whitland, Wales, UK). Magnetic pulses were delivered at a frequency of 1 Hz for 10 minutes, totaling 600 pulses. The stimulation intensity was consistently set at 55% of the maximum stimulator output for all participants. The stimulation intensity setting was chosen instead of the traditional motor threshold-based method, as evidence suggests that using motor thresholds is unsuitable for regions outside the motor cortex (Antal, Nitsche, Kincses, Lampe & Paulus, 2004; Turi et al., 2022; Wassermann, McShane, Hallett, & Cohen, 1992). Furthermore, the use of a uniform intensity setting has already proven to be effective in modulating SL in a previous study (Ambrus et al., 2020). Coil positioning followed the international 10-20 EEG system using an EEG cap, providing 90% accuracy in targeting the desired area (Herwig, Satrapi & Schönfeldt-Lecuona, 2003). The coil was placed over the F3 electrode for left DLPFC stimulation and the F4 electrode for right DLPFC stimulation (Brodmann 9) throughout the stimulation period. For bilateral DLPFC stimulation, the coil was positioned over the F3 for the first half (5 minutes, 300 pulses) and then moved to F4 for the second half (Fig. 1b). The stimulation order for each hemisphere was counterbalanced across participants in the Bilateral DLPFC group. During sham stimulation, the coil was tilted 90° away from the skull, ensuring that participants heard the machine's noise without any impact on brain activity.

Experimental design

The experiment took place over two consecutive days, with participants completing tasks in a well-lit, quiet environment. On the first day, participants performed the ASRT task across 25 blocks, taking around 25 to 30 minutes to learn an 8-element probabilistic sequence, followed by the learning phase of the PALT, which lasted about 10 minutes (Learning Session). On the same day, participants also completed the Counting Span Task to ensure that the four experimental groups were comparable in baseline cognitive functions (Table 2). After a 24-hour offline period, the second day included rTMS administration and a retest of participants' statistical and declarative knowledge (Retrieval Session). The rTMS lasted 10 minutes, followed by the ASRT task, which consisted of 5 blocks using the same probabilistic sequence practiced on day one, or the recall phase of the PALT. The order of the statistical and declarative learning tasks was counterbalanced across participants and sessions (Fig. 2a).

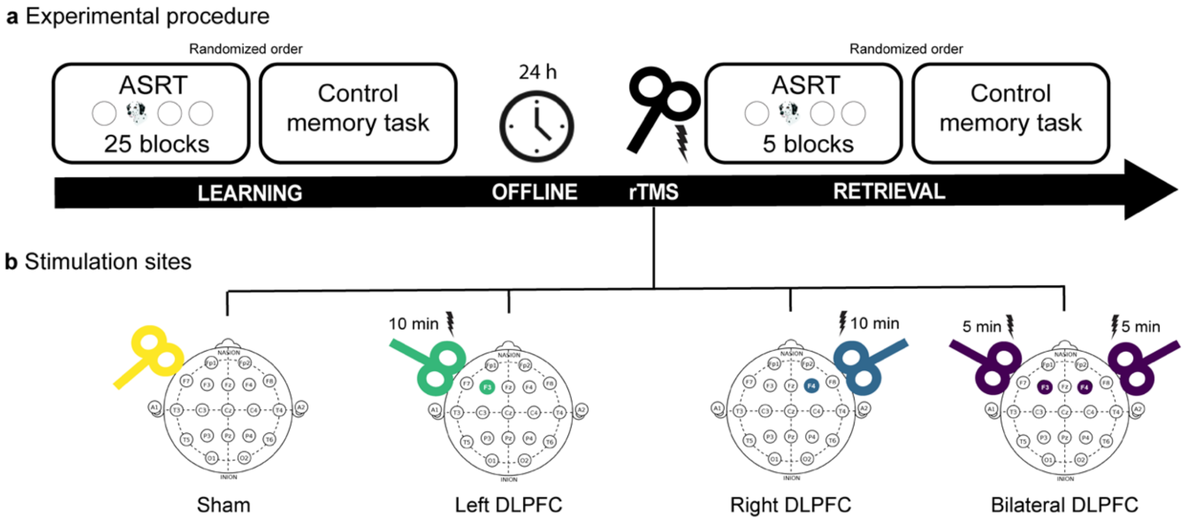

Figure 2. Study design. (a) The study took place over two consecutive days. On day one (Learning Session), participants completed 25 blocks of the ASRT task and the learning phase of the PALT, followed by a 24-hour offline period. On day two (Retrieval Session), participants received 10 minutes of 1 Hz rTMS and then performed 5 blocks of the ASRT task and the recall phase of the PALT. The order of the tasks was counterbalanced across participants on both days. (b) Stimulation sites for the four groups: The coil was tilted 90° in the Sham group, F3 was stimulated for 10 minutes in the Left DLPFC group, F4 for 10 minutes in the Right DLPFC group, and both F3 and F4 were sequentially stimulated for 5 minutes each in the Bilateral DLPFC group.

Data processing

In the case of the ASRT task, trials involving trills (e.g., 1–2–1) and repetitions (e.g., 1–1–1) were excluded from the analysis as participants may have inherent response patterns for these trial types. Additionally, trials with RTs below 100 ms or exceeding three SDs above the mean RT were removed, as these were considered invalid responses. Trials with incorrect responses (misses) were also excluded.

Regarding the PALT, three learning indices were derived from participants' responses. Item memory index was calculated by subtracting the ratio of incorrect Old-Old responses to New-New pair (false alarms) from the ratio of correct Old-Old rearranged pair responses (hit rate). Association learning index was quantified by subtracting the ratio of correct Old-Old rearranged pair responses (hit rate) from the ratio of correct original Old-Old responses (hit rate). Recollection index was defined by subtracting the ratio of incorrect Old-Old original responses to Old-Old rearranged pairs (false alarms) from the ratio of correct Old-Old original responses (hit rate).

Statistical analysis

Statistical analysis on block-wise mean RT data from the ASRT task was conducted in R using linear mixed models (LMMs) with the *afex* package, applied separately to the Learning and Retrieval Sessions. Fixed factors included Trial Type (high- vs. low-probability), Group (Left, Right, Bilateral, Sham), and Block (Learning Session: blocks 1–25; Retrieval session: blocks 26–30). Subject was included as a random intercept, with by-participant correlated slopes for the Block factor. To evaluate the factors influencing model quality, a likelihood ratio test was performed using the *anova* function in R. This test compared model likelihoods, based on Akaike Information Criterion (AIC), with the model showing the lowest AIC indicating the best fit (Bozdogan, 1987). Estimated marginal means were calculated using the *emmeans* package. On the other hand, comparing the three PALT learning indices across the four groups, ANOVAs were conducted. A significant level of 0.05 was used for all analyses, with Bonferroni correction applied to post hoc comparison where necessary.

Study II – Behavioral intervention to SL consolidation

Participants

This online study initially included 361 university students who participated in an exchange for course credit. After rigorous quality control of data (for details, see "*Data processing"*), the final sample comprised 268 participants (M_{AGE} = 21.46 years, SD_{AGE} = 2.20 years; 77.61% female). Participants were randomly assigned to one of three groups (15-second, 30-second, or self-paced), with no significant differences in age, education, sex, handedness, or working memory performance between groups (Table 3). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric conditions. Informed consent was obtained, and the study was approved by the Research Ethics Committee of Eötvös Loránd University (Budapest, Hungary), following the Declaration of Helsinki.

Table 3. Descriptive statistics of the three experimental groups

	Self-paced group (n = 88)	**15-second group (n = 90)**	**30-second group (n = 90)**	**Comparison**
Age (years)	21.89 ± 2.07	21.24 ± 2.23	21.27 ± 2.26	*p* = .09
Education (sec/BA/MA)	68/17/3	67/22/1	73/16/1	*p* = .56
Gender (m/f)	18/70	20/70	22/68	*p* = .82
Handedness (l/r/a)	8/80/0	8/80/2	10/78/2	*p* = .68
2-back task (d')	1.57 ± 0.95	1.49 ± 0.87	1.52 ± 0.89	*p* = .82

Notes. Mean and SD values for age and 2-back task are presented. For education (sec = secondary education or lower, BA = bachelor's level or equivalent, MA = master's level or equivalent), gender (m = male, f = female), and handedness (l = left, r = right, a = ambidextrous), case numbers are presented.

Stimuli

The ASRT task enabled us to assess both implicit SL and general skill learning separately. The task has already been described above. Participants were required to respond to a stream of visual stimuli (a Dalmatian's dog head) where pattern elements alternated with random ones (Fig. 3A) without the participants being aware. High- and low-probability triplets emerged from this probabilistic sequence (Fig. 3B). However, there are some differences between the versions of the task used in the two studies. The fundamental distinction is that the task was performed online in the participants' own environment rather than in a research laboratory. The task was programmed in JavaScript using the jsPsych framework (de Leeuw, 2015). Second, due to the online, unsupervised environment, practice blocks preceded the learning phase. Third, the four response keys corresponding to the four locations were S, F, J, and L on the participants' own computer keyboard. Finally, while in Study I, all participants proceeded in a self-paced manner, break durations were manipulated in this version (see in *Experimental design*). In all other respects, the task structure was identical to the previously described version.

Experimental design

The experiment was conducted online using the Gorilla Experiment Builder, ensuring precise stimulus presentation and response timing. Participants were randomly assigned to one of three task versions, differing only in the duration of between-block rest periods: (1) 15-second breaks, (2) 30-second breaks, or (3) self-paced breaks, allowing participants to proceed when they were ready (Fig. 3C). The task began with two practice blocks, followed by 25 learning blocks, each containing 80 trials, and took approximately 25-30 minutes to complete. Accuracy and RTs were recorded for each trial. After completing the ASRT task, participants' awareness of the sequence structure was assessed using a brief questionnaire and a task based on the process dissociation procedure, which differentiates explicit and implicit memory processes. The results of these tests showed that statistical knowledge remained equally implicit across all three groups. Lastly, participants completed 0-back and 2-back tasks to assess working memory.

Data processing

Before analysis, we applied exclusion criteria to ensure data reliability. Participants were excluded if they (1) had an accuracy below 80% on the ASRT task (34 participants), (2) scored below 60% on the 0-back task (eight participants), (3) failed to respond in the n-back tasks (16 participants), (4) restarted the experiment after quitting (four participants), (5) had prior ASRT experience (eight participants), or (6) delayed response after rest periods in at least five blocks (21 participants). Additionally, participants with an average RT over 1000 ms for the first trials of blocks were removed (nine from the 15-second group and 12 from the 30-second group). Since age distribution varied across groups, those older than 35 years were also excluded (11 participants).

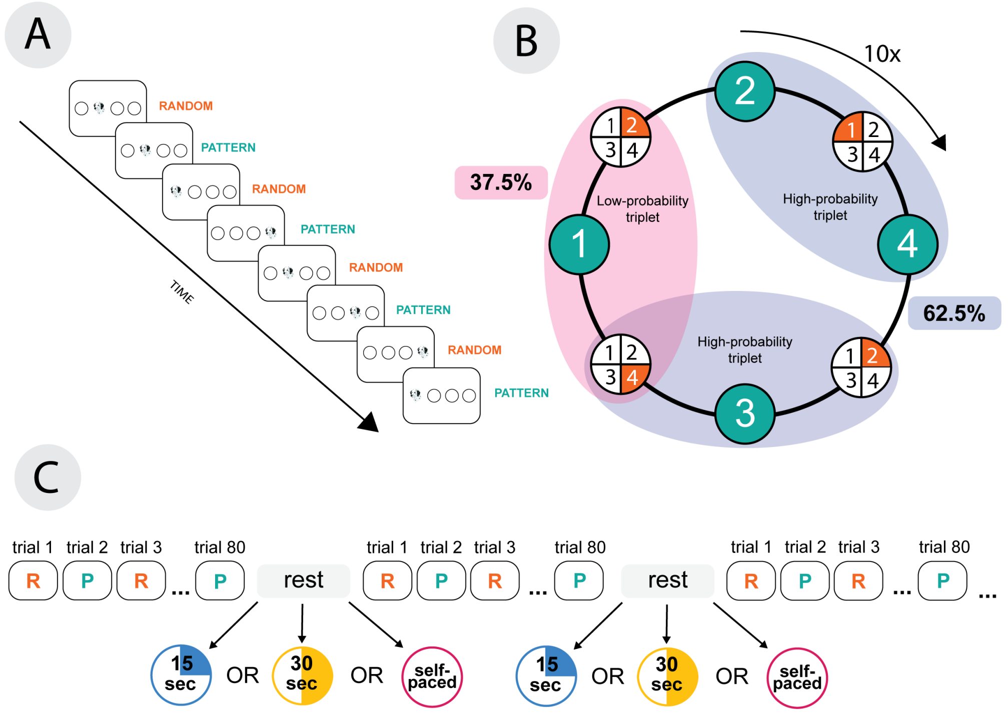

Figure 3. The ASRT task and the study design. (A) A visual stimulus (a Dalmatian dog's head) appeared in one of four horizontally arranged locations. The stimuli followed an eight-element probabilistic sequence, where fixed and pattern elements alternated with randomly assigned positions. (B) Each trial was classified as the third element of a three-item sequence (triplet). Due to the probabilistic structure, high-probability trials occurred more frequently (62.5% of trials), than low-probability trials (37.5%). (C) Each learning block contained 80 trials, repeating the sequence 10 times. Participants were divided into three groups based on the length of the between-block breaks: 15-second, 30-second, or self-paced.

After ensuring data quality, we removed inaccurate responses (misses), trills (e.g., 1–2–1), repetitions (e.g., 1–1–1), and trials with RTs over 1000 ms, excluding a total of 20.22% of trials. To smooth the data, ASRT blocks were grouped into units of five consecutive blocks. SL scores for each learning unit were measured by subtracting the median RT of high-probability trials from low-probability trials of the unit, then standardizing by dividing by mean RT. General skill learning was assessed using median RTs for each learning unit, independent of trial probability.

To analyze within-block (online) and between-block (offline) changes, each block of 80 trials was divided into five bins (16 trials each). SL scores based on the RT difference between high-probability and low-probability trials were calculated for each bin. Online SL was calculated as the change in learning scores from the first to the last bin within a block (change scores), averaged across all 25 blocks. Offline SL was measured as the difference between the last bin of one block and the first bin of the next (change scores), averaged across all 25 blocks. The same approach was used for general skill learning but based on median RTs regardless of trial type.

Statistical analysis

We conducted statistical analyses using JASP 0.16. Before the main statistical analyses, we calculated the average and median rest durations for the self-paced group. The mean was 16.67 s (*SD* = 25.48) and the median was 10.58 s. One-sample t-tests showed no significant difference from the 15-second group ($t(87) = 0.62$, $p = .54$) but a significant difference from the 30-second group ($t(87) = -4.91$, $p < .001$). To analyze the ASRT task, learning blocks were grouped into five larger units: blocks 1–5, blocks 6–10, blocks 11–15, blocks 16–20, and blocks 21–25. To compare SL across groups, we conducted a mixed-design one-way analysis of variance (ANOVA) with the within-subject factor of Blocks (block 1–5 vs. block 6–10 vs. block 11–15 vs. block vs. 16–20 vs. block 21–25) and the between-subjects factor of Group (self-paced, 15-second, 30-second), with SL scores as dependent variable. To test whether general skill learning (i.e., the overall speedup on the task) differed between groups, a similar mixed-design ANOVA was conducted but with median RT as the dependent variable. Additionally, mixed-design ANOVAs were used to analyze offline and online changes separately for both SL and general skill learning with the within-subjects factor of the Learning Phase (offline vs. online) and the between-subjects factor of Group (self-paced, 15-second, 30-second), with change scores as the dependent variable. A significant level of 0.05 was used for all analyses, with Bonferroni correction applied to post hoc comparison where necessary.

Results

Study I – Brain stimulation intervention to SL retrieval

Comparable SL performance in the four groups before rTMS

The optimal model included Trial Type, Block, and Group as fixed factors, with Block also serving as a by-participant random slope factor. A main effect of Trial Type was observed, with high-probability trials yielding faster RTs than low-probability trials, confirming that SL occurred across all participants ($F(1,4840) = 278.76$, $p < .001$). The Trial Type × Block interaction indicated a progressive enhancement in SL, as the difference between high- and low-probability triplets increased over time ($F(1,4840) = 33.62$, $p < .001$). However, there was no evidence of SL differences between the four groups, as neither the Group × Trial Type interaction ($F(3,4840) = 0.45$, $p = .714$) nor the Group × Block interaction ($F(3,4840) = 0.32$, $p = .814$) reached significance before stimulation (Fig. 4a, b). The main effect of Block showed decreasing RTs throughout the task, reflecting gradual general skill learning ($F(1,97) = 321.79$, $p < .001$). However, no group differences in general skills were found, as neither the main effect of Group ($F(3,97) = 0.05$, $p = 0.987$) nor the Group × Block interaction ($F(3,97) = 2.09$, $p = .106$) was significant.

Enhanced retrieval capacity of statistical knowledge after bilateral DLPFC inhibition

The optimal model for the Retrieval session included Trial Type and Group as fixed factors, along with their interaction, while Block was treated as a by-participant random slope factor. SL remained intact, as indicated by a significant main effect of Trial Type, with faster responses to high-probability trials compared to low-probability ones ($F(1,804) = 199.10$, $p < .001$). The absence of a main effect of Group suggested no significant differences in general skills between the four groups ($F(3,97) = 0.41$, $p = .743$). However, the Group × Trial Type interaction indicated a variation in SL performance among the groups ($F(3,804) = 3.62$, $p = .013$). Post hoc Welch's t-tests revealed that two stimulation groups outperformed the Sham group in SL: the Bilateral DLPFC group ($t(44.835) = 3.04$, $p < .01$) and the Left DLPFC group ($t(47.839) = 2.32$, $p < .05$). However, after correcting for multiple comparisons, only the Bilateral DLPFC group maintained significance (Fig. 4c, d).

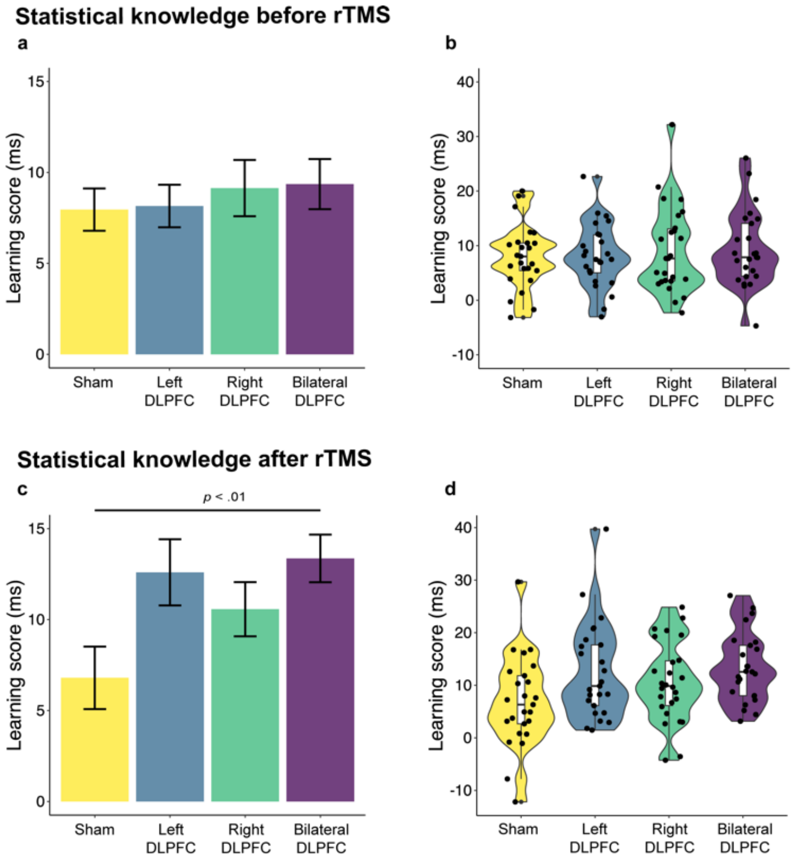

Figure 4. Statistical knowledge before and after rTMS. The y-axis represents the mean SL scores (RT difference between high- and low-probability trials in ms) for the four groups, where higher values indicate greater sensitivity to the underlying statistical structure. This measure reflects the extent to which participants responded faster to high-probability trials. Error bars indicate the standard error of the mean. (a) No significant differences in SL were found between the DLPFC groups and the Sham group in the Learning session. (b) Individual SL scores for each of the four groups. (c) The Bilateral DLPFC group showed significantly better retrieval of statistical knowledge than the Sham group ($p < .01$). (d) Individual SL scores for each of the four groups.

Comparable recall capacity of declarative knowledge after rTMS

The four groups exhibited similar declarative memory performance in the Retrieval Session, with no significant differences observed in the item memory index ($F(3, 97) = 0.85$, $p = .46$, $\eta^2p = 0.02$), association learning index ($F(3, 97) = 0.50$, $p = .67$, $\eta^2p = 0.01$), or recollection index ($F(3, 97) = 0.34$, $p = .79$, $\eta^2p = 0.01$).

Study II – Behavioral intervention to SL consolidation

Did rest period duration influence SL?

The ANOVA showed a gradual increase in learning scores across all participants, regardless of the rest period duration (main effect of Blocks: $F(4,1060) = 25.68$, $p < .001$, $\eta p^2 = 0.09$). Pairwise comparisons revealed no significant differences in learning between blocks 6–10 and blocks 11–15 ($p = .82$), between blocks 6–10 and blocks 16–20 ($p = .06$), between blocks 11–15 and blocks 16–20 ($p < .99$), or between blocks 16–20 and blocks 21–25 ($p = .19$). However, all other comparisons between block arrays were significant (all $p < .01$). This indicates that consecutive learning units did not differ significantly, but learning was observed between more temporally distant sections of the task. Importantly, there were no differences in SL between the three experimental groups (main effect of Group: $F(2,265) = 0.65$, $p = .53$, $\eta p^2 < 0.01$). The Blocks × Group interaction was also non-significant ($F(8,1060) = 0.28$, $p = .97$, $\eta p^2 < 0.01$), indicating that the three groups did not differ in the time course of SL either (Fig. 5A, C).

Did rest period duration influence general skill learning?

We observed a gradual decrease in RTs across the task (effect of Blocks: $F(2.73,723.72) = 275.21$, $p < .001$, $\eta p^2 = 0.51$). Pairwise comparisons indicated that each epoch significantly differed from the others (all $p < .01$), reflecting continuous learning throughout the blocks. The three groups showed significant differences in response times (main effect of Group: $F(2,265) = 8.69$, $p < .001$, $\eta p^2 = 0.06$), with the self-paced group responding more slowly than the 15-second and 30-second groups. The Blocks × Group interaction was also significant ($F(8,1060) = 2.33$, $p = .04$, $\eta p^2 = 0.02$). Pairwise comparisons revealed that RTs were significantly higher in the self-paced group compared to the 30-second group in blocks 6–10, 11–15, 16–20, and 21–25 (all $p < .01$). The self-paced group also showed significantly higher RTs compared to the 15-second group in these blocks (all $p < .01$). Thus, while all three groups had similar speeds in the first learning unit, the self-paced group began to slow down relative to the other two groups starting from the second learning unit (Fig. 5B, D).

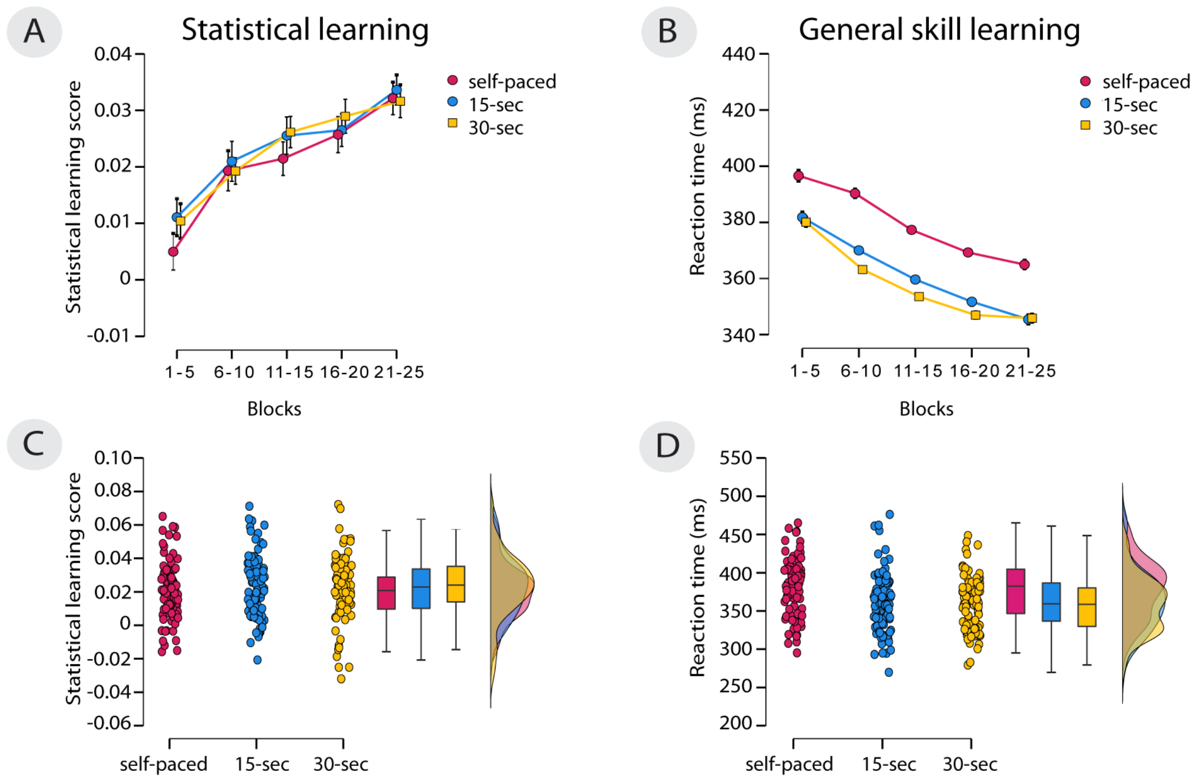

Figure 5. The effect of rest period duration on SL and general skill learning. Error bars represent the standard error of the mean. The x-axes show the experiment blocks or groups, while the y-axes show SL scores or RTs. (A) The temporal progression of SL scores across the three groups. All groups exhibited significant learning, but learning rates did not differ. (B) The temporal progression of general skill learning in the three groups. RTs decreased across all groups, with the self-paced group showing slower RTs than the 15-second and 30-second groups. (C) Individual SL scores (dots represent participant means). Boxplots and violin plots display the distribution of SL scores across the three groups. (D) Individual general RT scores (dots represent participant means). Boxplots and violin plots display the distribution of median RTs across the three groups.

How did rest period duration affect offline and online SL?

The ANOVA revealed a significant interaction between the Learning Phase and Group factors ($F(2,265) = 3.51$, $p = .03$, $\eta p^2 = 0.03$). Bonferroni-corrected post hoc comparisons showed that online and offline changes differed in the 15-second group ($p = .04$), with offline changes being significantly smaller than online changes. However, no main effect of Group ($F(2,265) = 1.60$, $p = .20$, $\eta p^2 = 0.01$) or Learning Phase ($F(2,265) = 2.50$, $p = .12$, $\eta p^2 < 0.001$) was observed (Fig. 6A). To determine whether online and offline learning occurred in the full sample and within each group, one-sample t-tests were conducted. In the full sample, online learning scores were significantly different from zero ($t(267) = 2.05$, $p < .05$), whereas offline learning scores were not ($t(267) = 1.11$, $p = .27$). In the self-paced group, neither online ($t(87) = -0.17$, $p = .86$) nor offline learning scores ($t(87) = 0.92$, $p = .36$) differed from zero. Similarly, in the 30-second group, neither online ($t(89) = 0.61$, $p = .55$) nor offline scores ($t(89) = -0.05$, $p = .96$) were significantly different from zero. However, in the 15-second group, both learning scores significantly deviated from zero: online learning scores were positive ($t(89) = 3.50$, $p < .001$), while offline learning scores were negative ($t(89) = -3.39$, $p < .01$). This suggests that participants in this group exhibited online learning but experienced forgetting offline. The absence of significant online and offline learning effects in the other two groups may be due to a balanced distribution of positive and negative learning scores within those groups (Fig. 7A–C).

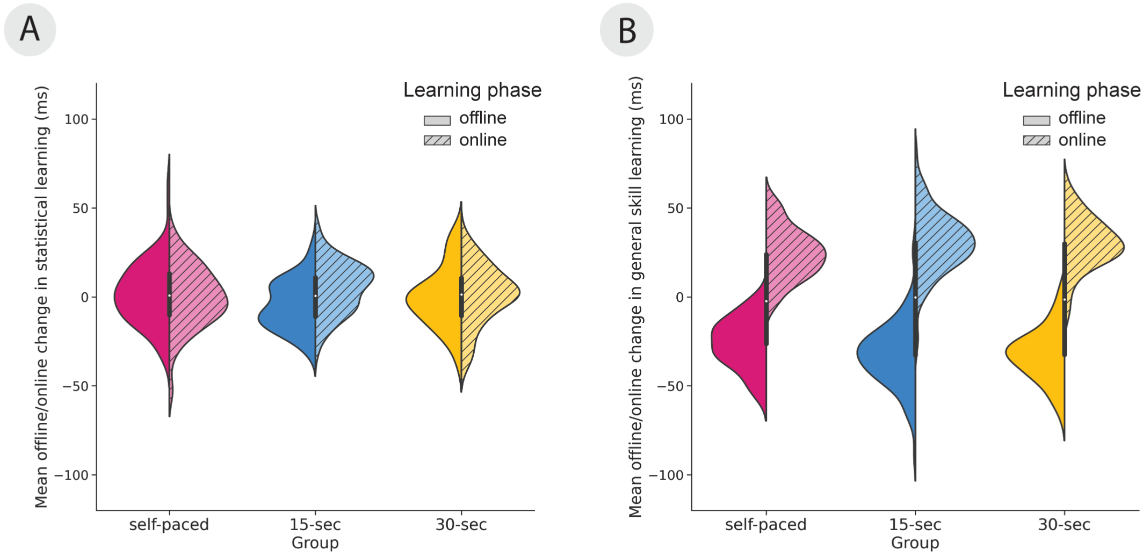

Figure 6. Offline vs. online changes in SL and general skills. The x-axes represent the three groups, and the y-axes show mean offline/online changes in ms. The violin plots display both offline changes (filled halves) and online changes (striped halves). (A) In the 15-second group, online changes were significantly greater than offline changes in SL. Online learning showed improvement, while offline changes indicated forgetting in this group. (B) General skill changes followed a similar pattern across groups, with acceleration after rest periods and deceleration during learning.

How did rest period duration affect offline and online general skill learning?

We observed a significant main effect of Learning Phase ($F(2,265) = 920.49$, $p < .001$, $\eta p^2 = 0.77$), with RTs slowing down during the blocks but speeding up following rest periods. No main effect of Group was detected ($F(2,265) = 0.02$, $p = .98$, $\eta p^2 < .001$). However, the interaction between Learning Phase and Group was significant ($F(2,265) = 4.38$, $p = .01$, $\eta p^2 = 0.03$). Despite this interaction, none of the between-group comparisons for online and offline changes remained significant after Bonferroni correction (all $p > 0.17$; Fig. 6B). One-sample t-tests confirmed that participants exhibited online learning ($t(267) = 29.14$, $p < .001$) but showed a decline in general skill performance during offline periods (*t*(267) = -30.60, *p* < .001) across the entire sample. This pattern was consistent across all three groups. Online general skill learning was observed in the self-paced group (*t*(87) = 15.87, *p* < .001), the 15-second group (*t*(89) = 16.35, *p* < .001), and the 30-second group (*t*(89) = 19.18, *p* < .001). During offline periods, performance declined in the self-paced group (*t*(87) = -17.16, *p* < .001), the 15-second group (*t*(89) = -16.78, *p* < .001), and the 30-second group (*t*(89) = -20.21, *p* < .001) (Fig. 7D–F).

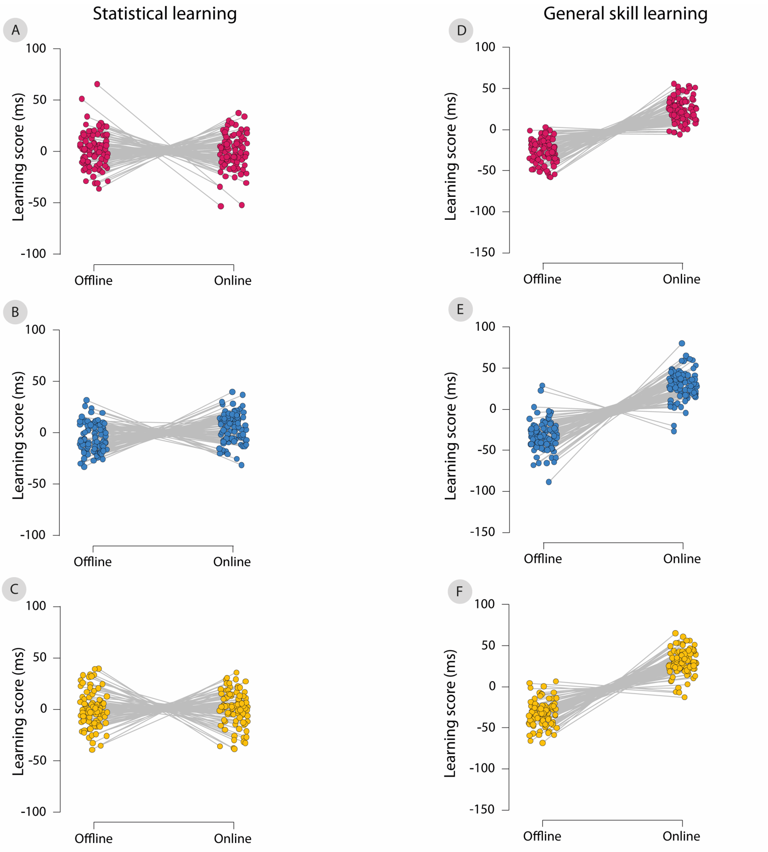

Figure 7. The dynamics of offline/online learning and forgetting in the four groups. The y-axes represent offline and online learning in ms, while the x-axes show individual mean learning scores. (A–C) Individual offline and online SL change scores for the self-paced (A), 15-second (B), and 30-second (C) groups. (D–F) Individual offline and online general skill change scores for the self-paced (D), 15-second (E), and 30-second (F) groups.

Discussion

This thesis summarizes the findings of two studies that aimed to modulate SL in its different phases through neuromodulation and behavioral interventions. Specifically, **Study I** (Brain stimulation study) addressed a gap in the literature on SL modulation through TMS. To our knowledge, no prior study has investigated the effect of TMS on access to statistical knowledge. We applied inhibitory rTMS over the left, right, or bilateral DLPFC (Brodmann 9) immediately before retesting participants' statistical knowledge acquired the day before and compared the performance of these real stimulation groups to a Sham group. Our findings revealed that bilateral DLPFC inhibition enhanced SL retrieval, as this group outperformed the Sham group. This effect was specific to SL retrieval, as rTMS over the DLPFC did not impact recall performance on a declarative memory task.

If we read a textbook on memory consolidation, we find that consolidation requires at least several hours to take place (Squire, Genzel, Wixted & Morris, 2015). However, it seems that, in some cases, even a few seconds may be sufficient. **Study II** (Behavioral study) investigated the role of this rapid consolidation in SL. We manipulated the length of short rest periods intervening in SL using a between-subjects design, comparing SL performance across three groups: 15-second, 30-second, and self-paced. While the length of these rest periods did not influence overall SL performance, it did affect an unrelated learning process, namely general skill learning. Participants in the self-paced group exhibited slower performance compared to the fixed-duration groups. We also examined whether offline and online SL differed between the three groups. Our results indicated that shorter rest periods (i.e., 15 seconds) led to SL occurring exclusively online, diminishing offline learning, while longer rest periods (i.e., 30 seconds) did not induce this learning pattern.

Enhancing the retrieval capacity of statistical learning through brain stimulation intervention

Our findings of **Study I** indicate that disrupting the DLPFC (Brodmann 9) enhances the retrieval capacity of SL, particularly when both hemispheres are inhibited. Importantly, this effect appears to be specific to SL, as general skills (i.e., the overall response speed) and performance on the control memory task remained unaffected. This specificity aligns with prior research suggesting that the DLPFC plays a pivotal role in modulating SL, although the exact nature of its influence remains debated (Szücs-Bencze et al., 2023). Earlier studies have yielded mixed results regarding DLPFC stimulation and SL outcomes. Some studies reported decreased SL following DLPFC stimulation (Pascual et al., 1996; Robertson, Tormos, Maeda & Pascual-Leone, 2001), while others observed improved learning after DLPFC disruption (Ambrus et al., 2020; Galea et al., 2010). This inconsistency likely stems from differences in stimulation protocols and timing. Notably, studies reporting reduced learning often employed excitatory rTMS (Pascuel-Leone et al., 1996) or inhibitory protocols applied before the learning phase (Robertson et al., 2001). Conversely, studies demonstrating enhanced learning typically applied inhibitory stimulation after the learning phase, facilitating consolidation and subsequent knowledge retention (Ambrus et al., 2020; Galea et al., 2010).

Our findings extend prior findings by demonstrating that DLPFC inhibition not only enhances the acquisition and consolidation of statistical regularities but also facilitates their retrieval. This conclusion is supported by previous work showing improved linguistic SL performance following DLPFC suppression through cTBS (Smalle et al., 2022; Smalle, Panouilleres, Szmalec & Möttönen, 2017). Additionally, Galea and colleagues (2010) found that post-training cTBS over the DLPFC improved non-linguistic motor sequence learning, particularly when the right hemisphere was targeted. Similarly, another study reported offline improvements in SL after right DLPFC inhibition (Tunovic, Press & Robertson, 2014).

In our study, only bilateral DLPFC inhibition significantly enhanced retrieval, suggesting that simultaneous modulation of both hemispheres is necessary to overcome potential compensatory mechanisms (Ambrus et al., 2020). Interestingly, while left DLPFC inhibition also improved retrieval compared to the Sham group, this effect did not reach statistical significance after correcting for multiple comparisons. This may be due to interhemispheric compensation, where the unstimulated hemisphere counteracts the effects of unilateral inhibition. Additionally, differences in task complexity may influence the effectiveness of lateralized stimulation. In our study, inhibition of the right DLPFC was the least effective in enhancing retrieval, which contrasts with findings from studies using simpler, deterministic sequences (Galea et al., 2010; Tunovic et al., 2014). The more complex probabilistic sequences in our study likely engage broader neural circuits, with a stronger reliance on the left hemisphere. This hypothesis is further supported by those studies where the acquisition of complex linguistic sequences was successfully improved by left DLPFC inhibition (Smalle et al., 2017, 2022).

One possible framework for interpreting our findings is the competition theory, which posits that different cognitive systems compete for shared neural resources (Borragán, Slama, Destrebecqz & Peigneux, 2016; Gillan et al., 2011; Poldrack & Packard, 2003). Within this model, the DLPFC serves as a regulatory hub, balancing the competition between executive control processes and habitual learning mechanisms. The PFC primarily supports goal-directed behavior, including working memory and executive functions, while simultaneously inhibiting automatic, associative learning (Juhasz, Nemeth & Janacsek, 2019; Smalle & Möttönen, 2023). During SL, being linked to the habitual system, repeated exposure can lead to automaticity, transitioning from goal-directed learning (involving the PFC) to habit-based processing (dominated by the striatum). Consequently, reducing DLPFC involvement allows greater cognitive resources to be allocated toward SL processes. This competitive dynamic has been consistently observed across various experimental manipulations. For instance, interventions that suppress PFC activity—such as hypnosis (Nemeth et al., 2013b), TMS (Ambrus et al., 2020), or cognitive overload (Smalle et al., 2022)—have been shown to enhance SL performance. Neuroimaging studies further support this model, indicating that diminished PFC engagement promotes habitual, bottom-up learning processes (Tóth et al., 2017; Park et al., 2022).

Competition may also manifest within the hippocampal system, where both episodic memory and SL rely on overlapping neural circuits (Sherman, Turk-Browne & Goldfarb, 2024). The DLPFC exerts inhibitory control over the hippocampus, modulating retrieval processes (Benoit et al., 2015; Oehrn et al., 2018; Woodcock et al., 2015). However, if the DLPFC functions as a domain-general controller, its inhibition should theoretically affect both statistical and episodic retrieval. Our study did not observe such an effect in the control memory task. This discrepancy may be attributed to the nature of the episodic task, which involved incidental learning with intentional retrieval. Prior research suggests that DLPFC engagement during episodic retrieval is strategy-dependent (Kim, 2010; Manenti, Cotelli, Calabria, Maioli & Miniussi, 2010), implying that tasks requiring minimal strategic processing may not engage DLPFC-dependent mechanisms robustly. Future research should employ more complex and strategically demanding episodic tasks to further explore the interaction between these memory systems and the role of the PFC in mediating their competition.

Alternatively, our results may reflect the strengthening of the frontostriatal network rather than direct competition between cognitive systems. Cognitive processes are supported by extensive neural networks, and neuromodulation techniques like rTMS may induce broad changes beyond the targeted brain regions (Bergmann & Gartwigsen, 2021; Beynel, Powers & Appelbaum, 2020). SL, in particular, relies on the functional interplay between the PFC and the basal ganglia—a network collectively known as the frontostriatal system (Janacsek et al., 2020; Naismith et al., 2010; Reber, 2013). Reduced DLPFC engagement may optimize conditions within the frontostriatal network, facilitating more efficient SL and its retrieval processes (Park et al., 2020; Tóth et al., 2017). This perspective suggests that the observed effects result from enhanced network dynamics rather than direct competition between memory systems.

Enhancing the consolidation capacity of statistical learning through behavioral intervention

The main finding of **Study II** concerns the differential effects of rest period length on the offline and online phases of SL. We found evidence for the beneficial effect of longer rest periods compared to shorter ones, as learning deteriorated during the offline phases in the latter case, while with longer breaks, learning remained balanced during both the offline and online phases. Our findings on SL dynamics only partially replicated previous research. Prior studies indicated that SL occurs primarily online, while forgetting happens offline during rest periods (Fanuel et al., 2022; Quentin et al., 2021). We found evidence for this pattern only in the 15-second group, where SL was confined to online periods with little to no offline improvement. However, this clear dissociation was not observed in the 30-second and self-paced groups.

One possible explanation stems from the role of neural replay in rapid consolidation (Buch, Claudino, Quentin, Bönstrup & Cohen, 2021). It is plausible that the longer rest periods in the 30-second and self-paced groups allowed for sufficient time for neural replay, facilitating both online learning and rapid consolidation. Conversely, the 15-second rest period may have been too brief to permit effective neural replay, thereby limiting offline gains. This interpretation is supported by a study that found offline improvement in probabilistic sequence learning with rest periods of two minutes between blocks (Prashad, Du & Clark, 2021), suggesting that a longer rest period may be necessary to observe offline benefits. An alternative explanation for the absence of clear offline learning effects in the 30-second and self-paced groups may be related to the experimental context. Participants completed the task in their own environments rather than in a laboratory setting. This may have reduced stress levels compared to in-lab testing. However, the limited rest period in the 15-second group may have increased stress levels, mimicking laboratory conditions. Given that stress can modulate SL (Tóth-Fáber et al., 2021a), participants in the 15-second group may have been more motivated to optimize performance during the task itself rather than relying on offline consolidation.

In general skill learning, we observed that performance improved online (i.e., during practice within blocks) and deteriorated offline (i.e., during rest periods between blocks). This pattern was consistent regardless of rest period length. This result regarding the dynamics of general skills (whether it occurs offline vs. online) aligns with previous studies (Fanuel et al., 2022; Quentin et al., 2021) and suggests that the dynamics of general skill acquisition are not influenced by the length of brief rest periods.

On the other hand, our findings of **Study II** suggest that the length of short rest periods influences SL and general skill learning in distinct ways. Our results indicate that the duration of these rest periods does not have a significant effect on overall SL performance across the task. This finding contrasts with the results of previous studies showing that short, 10-second rest periods facilitated motor skill learning and that even shorter rest periods continued to enhance performance (Bönstrup et al., 2019; Bönstrup, Iturrate, Hebart, Censor & Cohen, 2020). However, their task did not separate the subprocesses of learning, such as SL and general skill learning, making it difficult to determine which aspect was primarily affected. However, our findings are consistent with those of Fanuel and colleagues (2022), who also measured SL and found no significant effect of rest period length on overall performance. This discrepancy highlights the importance of distinguishing between SL and general skill learning when interpreting the impact of rapid consolidation.

Regarding general skill learning, participants in the self-paced condition, where they controlled the duration of their rest periods, exhibited slower RTs compared to the 15-second and 30-second fixed-duration groups. This suggests that the voluntary nature of the self-paced condition, rather than the actual rest duration, may be responsible for the observed differences in general skill performance. Although the average rest period length in the self-paced group was similar to that of the 15-second group, the two groups still differed significantly in their overall speed. The substantial variability in rest duration, reflected by the high SD in the self-paced group, further supports the notion that the critical factor may be whether the rest period is voluntary or compulsory. We propose that participants in the fixed-duration groups may have experienced a greater sense of urgency due to the imposed time limit, leading to faster RTs compared to the self-paced group.

Nevertheless, the lack of significant differences in overall SL outcomes between the three groups suggests that the rest period length primarily influences the dynamics of learning (i.e., whether it occurs offline or online) rather than the final level of statistical knowledge acquired.

Table 4. The main research questions and summary of findings

		Research question	Results
Study I	a.	Does inhibitory TMS over the DLPFC modulate the retrieval phase of SL?	DLPFC inhibition leads to enhanced retrieval of statistical knowledge
	b.	Does the effect of DLPFC inhibition on retrieval differ based on hemispheric lateralization (left, right, or bilateral stimulation)?	Bilateral stimulation reaches the most pronounced effect on SL retrieval
Study II	a.	How does short rest periods of different length affect SL performance?	The length of short rest periods does not impact overall SL performance
	b.	Does rest period length influence SL differently in online (within-block) and offline (between-block) phases?	Shorter rest periods shift SL to the online phase

Theoretical and methodological significance of the two studies

The field of SL research is currently facing a crisis characterized by the coexistence of multiple competing theories without a unified framework to explain the underlying neurocognitive mechanisms. This crisis can be attributed to three primary factors: the lack of robust phenomena, the instability of construct validity, and the difficulty of establishing casual relationships (Jenkins, Conway, Singh, Milne & Wilson, 2025). The present studies address all three problematic factors, providing important contributions to the field.

First, the demonstration of robust phenomena requires replicability—the ability to observe consistent effects over time and across different methodologies. **Study I** showed that SL can be reliably modulated through inhibitory stimulation of the DLPFC, independent of the learning modality (linguistic vs. non-linguistic) and the TMS protocol (rTMS vs. cTBS)

(Ambrus et al., 2020; Smalle et al., 2022). This replicability across experimental contexts strengthens the claim that the DLPFC plays a critical role in regulating SL processes. However, our research went one step further than replicating previous observations by examining an overlooked phase, namely retrieval. That is, we simultaneously confirmed the antagonistic role of the DLPFC in SL and, as a new result, showed that this is true not only for the acquisition and consolidation phase but also for the retrieval phase. Furthermore, **Study II** contributed to the robustness of the psychological phenomenon of rapid consolidation. Consolidation theories traditionally emphasize that consolidation takes hours, sometimes days, to occur (Squire et al., 2015). However, thanks to a discovery, consolidation research has taken a new direction in recent years, showing that consolidation can occur in seconds (Bönstrup et al., 2019). Our study adds to the evidence by revealing that such rapid consolidation occurs online. However, it also adds new knowledge to this area, as we have shown that the length of the rest periods influences which phases of learning benefit from this rapid consolidation: if the break is long enough, rapid consolidation occurs not only online but also offline, during the short breaks between the blocks.

Second, the studies address the issue of construct validity by disentangling SL and general skill learning. Prior research often conflates these processes, making it difficult to ascertain whether observed effects pertain specifically to SL mechanisms. In **Study I**, the finding that DLPFC inhibition selectively enhances SL while leaving general skill performance unchanged supports the notion that these have distinct cognitive constructs. Similarly, control memory task measuring declarative recall remained intact after rTMS, suggesting distinct neurocognitive mechanisms behind the two constructs. Furthermore, **Study II** demonstrated that rest period length differentially impacts SL and general skills, reinforcing the validity of treating these processes as separate entities. However, these results need to be replicable even when performing other SL paradigms. Different SL paradigms in different modalities or complexity are likely to require different neural networks and thus underlying cognitive processes, so it is conceivable that other paradigms would respond differently to DLPFC inhibition or to rest period manipulation. Nevertheless, it is important to distinguish between measuring different processes or simply not being replicable (i.e., not being robust).

Third, the difficulty of establishing causal relationships is a major obstacle in cognitive neuroscience. Both studies employ experimental manipulations (brain stimulation and rest period duration) that allow for causal inferences. **Study I** provides causal evidence that the

DLPFC directly modulates the retrieval capacity of SL. By showing the causal role of the DLPFC, an indirect relationship between SL and DLPFC-supported executive functions and working memory was demonstrated. This further supports studies reporting an antagonistic relationship between the two cognitive processes (Nemeth et al., 2013b; Pedraza et al., 2024; Virag et al., 2015). On the other hand, **Study II** demonstrates that altering rest period length can causally influence the dynamics of SL. These findings not only clarify the mechanisms of SL but also provide a foundation for future research aimed at further elucidating these causal pathways.

When discussing the 'theoretical crisis' in SL research, our findings provide critical insights into how DLPFC modulates memory systems. Specifically, our results align with predictive coding frameworks, which propose that the brain constantly generates and updates internal models of the environment based on sensory input. By inhibiting the DLPFC, we may reduce the brain's reliance on top-down predictions, thereby facilitating the retrieval of statistical regularities without interference from higher-order cognitive processes. Furthermore, our findings challenge classical dual-process theories, which often posit a clear distinction between implicit and explicit learning systems.

The methodologies employed in the presented studies offer innovative approaches to investigating the neurocognitive mechanisms underlying SL and provide new tools for addressing long-standing questions in the field. TMS studies often stimulate only one hemisphere or both hemispheres in separate groups (Szücs-Bencze et al., 2023). Bilateral stimulation—simultaneous or sequential stimulation of both hemispheres—is quite rare in the literature. The main strength of **Study I** is that it used both unilateral and bilateral approaches within a single research design. By comparing bilateral, left, and right DLPFC inhibition conditions, the study provides nuanced insights into hemispheric contributions to SL processes. Bilateral stimulation can be particularly useful when using SL paradigms that require the use of both hands. Another advantage is that it may eliminate compensatory mechanisms from the non-stimulated hemisphere. Additionally, the use of a control memory task ensures that the observed effects are specific to SL rather than general cognitive functions, enhancing the specificity and interpretability of the results.

In **Study II**, we employed a behavioral intervention manipulating rest period duration to investigate the temporal dynamics of SL and general skill acquisition. On the one hand, compared to Study I, we introduced a much more refined and sophisticated level of analysis that allows for distinguishing between offline and online learning phases. In addition, by systematically comparing fixed and self-paced conditions, the study provides a more comprehensive view of how rest duration influences learning dynamics. Since the effect of rest period duration was not shown on the overall learning index but was shown on the dynamics of learning (offline vs. online), it seems particularly important to include in analyses not only overall learning outcomes but also indicators measuring the active dynamics of learning, in order to be able to detect subtle effects.

Applied significance of the two studies

Although the studies presented in this thesis are primarily basic or fundamental research, investigating the processes and neural mechanisms of SL in healthy individuals, they also have implications for enhancing learning and memory processes, with potential application in clinical interventions, education settings and cognitive enhancement strategies.

Clinically, the findings of **Study I** indicate that targeted neuromodulation of the DLPFC may serve as a potential intervention for individuals with learning and memory deficits. TMS is already recognized and approved by the US Food and Drug Administration as a therapeutic tool, particularly for psychiatric conditions where well-defined neural alterations underlie the symptoms (e.g., depression, obsessive-compulsive disorder). Ongoing research explores the potential of TMS to alleviate cognitive symptoms of post-stroke conditions as well, with varying success (Shen, Hu, Feng, Li, & Wang, 2022). Our study highlights the importance of bilateral stimulation for achieving maximal effects, which could guide the development of more effective brain stimulation protocols in clinical practice. Compared to the standard TMS protocol for depression, which facilitates the left DLPFC due to its reduced activity, bilateral stimulation may be more beneficial in post-stroke or trauma-related rehabilitation for restoring cognitive and motor skills.

In an educational context, the results of **Study II** suggest that optimizing rest period length can improve learning outcomes. Specifically, longer rest intervals facilitate the rapid consolidation of statistical knowledge, which may inform the design of more effective learning schedules. This has practical relevance for educational programs aimed at enhancing procedural learning, such as language acquisition and skill training.

From a broader perspective, these studies contribute to the growing field of cognitive enhancement. The demonstration that both neural and behavioral interventions can modulate SL provides a foundation for developing novel strategies to improve cognitive performance. This is particularly relevant in populations with compromised cognitive functions, where enhancing SL could improve adaptive behavior and overall cognitive functioning. Some theories presume SL is an age-invariant cognitive mechanism; however, some think that SL deteriorates with age. In our aging society, it is predominantly important to keep our elderly in good cognitive shape, enabling them to rest in their environment as long as possible and postpone the need for hospitalization.

Limitations and future directions

While our findings of **Study I** provide compelling evidence that DLPFC inhibition enhances the retrieval of statistical knowledge, the underlying cognitive and neural mechanisms remain unclear. One crucial area for future exploration is the relationship between task complexity, lateralization, and DLPFC involvement. Our study suggests that bilateral DLPFC inhibition is more effective than unilateral stimulation, although left DLPFC inhibition also seemed to be beneficial. Precise mechanisms driving this lateralized effect require further investigation. Studies that manipulate task complexity systematically (e.g., deterministic vs. probabilistic sequences) while varying stimulation protocols across hemispheres may clarify how the DLPFC's lateralized functions contribute to the retrieval of SL. Additionally, while the competition model offers a plausible explanation for our findings, its applicability across different memory systems remains uncertain since recall capacity on a control memory task measuring declarative recall remained unaffected by DLPFC inhibition. Future studies should examine whether more cognitively demanding episodic memory tasks elicit DLPFC-mediated competitive interactions.

Another promising avenue involves the integration of functional neuroimaging with neuromodulation techniques to further explore the dynamics of the frontostriatal network. By combining these methodologies, future studies could map the specific neural circuits affected by DLPFC inhibition and how these changes influence the acquisition and retrieval of statistical knowledge. Such work could also identify whether the observed enhancement stems from altered connectivity patterns or direct effects on cognitive resource allocation.

A key limitation of **Study II** is that we measured SL during a single session. It remains unclear whether the effects of rest period duration on SL would become more pronounced over an extended learning period. Future research should investigate how rest period length influences SL across multiple sessions to capture potential long-term effects. Moreover, during an extended learning period, the effect of short rest periods on higher-order cognitive processes, such as higher-order sequence learning, could be examined (Nemeth et al., 2013a; Tóth-Fáber et al., 2021b; Kóbor et al., 2018). Additionally, our study only utilized brief rest periods of 15 and 30 seconds, while previous research demonstrating offline improvements in SL used much longer rest periods (e.g., two minutes; Prashad et al., 2021). Future studies should employ a broader range of rest period durations to determine the minimum time required to facilitate rapid consolidation and offline improvement. Directly manipulating the number of neural replays during these rest periods could provide a more comprehensive understanding of how brief breaks influence learning and memory processes.

Future studies should also tackle the role of individual characteristics in the dynamics of SL. In two groups (self-paced and 30-second) in our research, we found that the number of participants who learned or forgot during the offline and online phases was balanced. Future research could further investigate which psychological factors (e.g., stress, working memory) determine whether an individual primarily learns during the offline or online phases.

The combinations of Study I and Study II could further deepen our knowledge of the consolidation and retrieval processes of SL. On the one hand, extending the analysis of the brain stimulation study and examining the effect of rTMS not only to the aggregate learning output but also to the fine-grained offline and online phases would add a more nuanced picture of the role of the DLPFC in SL retrieval. On the other hand, it would be noteworthy to examine whether rest periods of different lengths would result in different retrieval efficiencies.

Conclusion

The studies presented here hold theoretical, methodological, and applied significance. From a theoretical perspective, our findings contributed to a deeper understanding of the less-explored phases of SL—namely, consolidation and retrieval. Regarding methodology, we introduced approaches that can grasp these processes more comprehensively. Regarding their applied significance, different methods are outlined to optimize SL processes in both healthy and clinical populations.

Study I (Brain stimulation study) has theoretical implications by demonstrating the functional role of the DLPFC in the retrieval of SL. Methodologically, it highlights that bilateral stimulation of brain regions may yield a greater effect than unilateral stimulation. In terms of applied relevance, these findings contribute to the development of strategies for facilitating SL processes in concerned clinical populations.

Study II's (Behavioral study) theoretical implication is that the length of short rest intervals differentially affects the distinct yet parallel processes of learning and consolidation, specifically SL and general skill learning. While the overall SL outcome was not influenced by the duration of rest intervals, these intervals had differential effects on the online and offline phases of SL. Methodologically, this implies that measuring the temporal dynamics of learning provides more nuanced insights than relying solely on an aggregate learning score. From an applied perspective, our findings can inform the design of task structures that effectively support both the online and offline phases of learning.

Together, these studies advance our understanding of the neurocognitive mechanisms underlying different phases of SL and offer valuable insights for optimizing the process of SL through interventions like task design manipulation and the application of neuromodulation techniques.

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References

Ambrus, G. G., Vékony, T., Janacsek, K., Trimborn, A. B., Kovács, G., & Nemeth, D. (2020). When less is more: Enhanced statistical learning of non-adjacent dependencies after disruption of bilateral DLPFC. *Journal of Memory and Language, 114*, 104144.

Andoh, J., & Martinot, J. L. (2008). Interhemispheric compensation: a hypothesis of TMS-induced effects on language-related areas. *European Psychiatry, 23*(4), 281-288.

Antal, A., Nitsche, M. A., Kincses, T. Z., Lampe, C., & Paulus, W. (2004). No correlation between oving phosphene and motor thresholds: a transcranial magnetic stimulation study. *Neuroreport, 15*(2), 297-302.

Arciuli, J. (2017). The multi-component nature of statistical learning. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1711), 20160058.

Ashby, F. G., & Crossley, M. J. (2012). Automaticity and multiple memory systems. *Wiley Interdisciplinary Reviews: Cognitive Science, 3*(3), 363-376.

Bennett, I. J., Madden, D. J., Vaidya, C. J., Howard Jr, J. H., & Howard, D. V. (2011). White matter integrity correlates of implicit sequence learning in healthy aging. *Neurobiology of Aging, 32*(12), 2317-e1.

Benoit, R. G., Hulbert, J. C., Huddleston, E., & Anderson, M. C. (2015). Adaptive top–down suppression of hippocampal activity and the purging of intrusive memories from consciousness. *Journal of Cognitive Neuroscience, 27*(1), 96-111.

Bergmann, T. O., & Hartwigsen, G. (2021). Inferring causality from noninvasive brain stimulation in cognitive neuroscience. *Journal of Cognitive Neuroscience, 33*(2), 195-225.

Berns, G. S., McClure, S. M., Pagnoni, G., & Montague, P. R. (2001). Predictability modulates human brain response to reward. *Journal of Neuroscience, 21*(8), 2793-2798.

Beynel, L., Powers, J. P., & Appelbaum, L. G. (2020). Effects of repetitive transcranial magnetic stimulation on resting-state connectivity: a systematic review. *Neuroimage, 211*, 116596.

Borragan, G., Slama, H., Destrebecqz, A., & Peigneux, P. (2016). Cognitive fatigue facilitates procedural sequence learning. *Frontiers Human Neuroscience, 10*(86).

Bozdogan, H. (1987). Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. *Psychometrika, 52*(3), 345-370.

Bönstrup, M., Iturrate, I., Hebart, M. N., Censor, N., & Cohen, L. G. (2020). Mechanisms of offline motor learning at a microscale of seconds in large-scale crowdsourced data. *NPJ Science of Learning, 5* (1), Article 7.

Bönstrup, M., Iturrate, I., Thompson, R., Cruciani, G., Censor, N., & Cohen, L. G. (2019). A rapid form of offline consolidation in skill learning. *Current Biology, 29*(8), 1346-1351.

Breton, J., & Robertson, E. M. (2017). Dual enhancement mechanisms for overnight motor memory consolidation. *Nature Human Behaviour, 1*(6), 0111.

Buch, E. R., Claudino, L., Quentin, R., Bönstrup, M., & Cohen, L. G. (2021). Consolidation of human skill linked to waking hippocampo-neocortical replay. *Cell Reports, 35*(10).

Clark, G. M., Barham, M. P., Ware, A. T., Plumridge, J., O'Sullivan, B., Lyons, K., Fitzgibbon, T., Buck, B., Youssef, G. J., Ullman, M. T., Enticott, P. G., & Lum, J. A. (2019). Dissociable implicit sequence learning mechanisms revealed by continuous theta-burst stimulation. *Behavioral Neuroscience, 133*(4), 341.

Clerget, E., Poncin, W., Fadiga, L., & Olivier, E. (2012). Role of Broca's area in implicit motor skill learning: evidence from continuous theta-burst magnetic stimulation. *Journal of Cognitive Neuroscience, 24*(1), 80-92.

Conway, C. M. (2020). How does the brain learn environmental structure? Ten core principles for understanding the neurocognitive mechanisms of statistical learning. *Neuroscience & Biobehavioral Reviews, 112*, 279-299.

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of tactile, visual, and auditory sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(1), 24.

De Leeuw, J. R. (2015). jsPsych: A JavaScript library for creating behavioral experiments in a Web browser. *Behavior Research Methods, 47*, 1-12.

Destrebecqz, A., & Cleeremans, A. (2005). Dissociating neural correlates of conscious and unconscious sequential learning. *Journal of Cognitive Neuroscience, 17*(4), 629-641.

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., Lehéricy, S., & Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199*(1), 61-75.

Du, Y., Prashad, S., Schoenbrun, I., & Clark, J. E. (2016). Probabilistic motor sequence yields greater offline and less online learning than fixed sequence. Frontiers in Human *Neuroscience, 10*, 87.

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex, 23*(10), 2467-2478.

Durrant, S. J., Taylor, C., Cairney, S., & Lewis, P. A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia, 49*(5), 1322-1331.

Fanuel, L., Pleche, C., Vékony, T., Janacsek, K., Nemeth, D., & Quentin, R. (2022). How does the length of short rest periods affect implicit probabilistic learning? *Neuroimage: Reports, 2*(1), 100078.

Farkas, B. C., Krajcsi, A., Janacsek, K., & Nemeth, D. (2024). The complexity of measuring reliability in learning tasks: An illustration using the Alternating Serial Reaction Time Task. *Behavior Research Methods, 56*(1), 301-317.

Fischer, S., Hallschmid, M., Elsner, A. L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences, 99*(18), 11987-11991.

Fiser, J., & Aslin, R. N. (2001). Unsupervised statistical learning of higher-order spatial structures from visual scenes. *Psychological Science, 12*(6), 499-504.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*(3), 458.

Frost, R., Armstrong, B. C., Siegelman, N., & Christiansen, M. H. (2015). Domain generality versus modality specificity: The paradox of statistical learning. *Trends in Cognitive Sciences, 19*(3), 117–125.

Galea, J. M., Albert, N. B., Ditye, T., & Miall, R. C. (2010). Disruption of the dorsolateral prefrontal cortex facilitates the consolidation of procedural skills. *Journal of Cognitive Neuroscience, 22*(6), 1158-1164.

Gillan, C. M., Papmeyer, M., Morein-Zamir, S., Sahakian, B. J., Fineberg, N. A., Robbins, T. W., & de Wit, S. (2011). Disruption in the balance between goal-directed behavior and habit learning in obsessive-compulsive disorder. *American Journal of Psychiatry, 168*(7), 718-726.

Hallgató, E., Győri-Dani, D., Pekár, J., Janacsek, K., & Nemeth, D. (2013). The differential consolidation of perceptual and motor learning in skill acquisition. *Cortex, 49*(4), 1073-1081.

Henin, S., Turk-Browne, N. B., Friedman, D., Liu, A., Dugan, P., Flinker, A., Doyle, W., Devinsky, O., & Melloni, L. (2021). Learning hierarchical sequence representations across human cortex and hippocampus. *Science Advances, 7*(8), eabc4530.

Herwig, U., Satrapi, P., & Schönfeldt-Lecuona, C. (2003). Using the international 10-20 EEG system for positioning of transcranial magnetic stimulation. *Brain Topography, 16*, 95-99.

Horváth, K., Török, C., Pesthy, O., Nemeth, D., & Janacsek, K. (2020). Divided attention does not affect the acquisition and consolidation of transitional probabilities. *Scientific Reports, 10*(1), 22450.

Howard Jr, J. H., & Howard, D. V. (1997). Age differences in implicit learning of higher order dependencies in serial patterns. *Psychology and Aging, 12*(4), 634.

Howard, D. V., Howard Jr, J. H., Japikse, K., DiYanni, C., Thompson, A., & Somberg, R. (2004). Implicit sequence learning: effects of level of structure, adult age, and extended practice. *Psychology and Aging, 19*(1), 79.

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron, 45*(2), 201-206.

Huang, Y. Z., Lu, M. K., Antal, A., Classen, J., Nitsche, M., Ziemann, U., Ridding, M., Hamada, M., Ugawa, Y., Jaberzadeh, A. P., Paulus, W., & Rothwell, J. (2017). Plasticity induced by non-invasive transcranial brain stimulation: a position paper. *Clinical Neurophysiology, 128*(11), 2318-2329.

Hunt, R. H., & Aslin, R. N. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General, 130*(4), 658–680.

Janacsek, K., Fiser, J., & Nemeth, D. (2012). The best time to acquire new skills: Age-related differences in implicit sequence learning across the human lifespan. *Developmental Science, 15*(4), 496-505.

Janacsek, K., & Nemeth, D. (2012). Predicting the future: from implicit learning to consolidation. *International Journal of Psychophysiology, 83*(2), 213-221.

Janacsek, K., Shattuck, K. F., Tagarelli, K. M., Lum, J. A., Turkeltaub, P. E., & Ullman, M. T. (2020). Sequence learning in the human brain: A functional neuroanatomical meta-analysis of serial reaction time studies. *NeuroImage, 207*, 116387.

Jenkins, H., Conway, C., Singh, S., Milne, A., & Wilson, B. (2025). Addressing the Theory Crisis in Statistical Learning Research. *PsyArXiv Preprints.*

Juhasz, D., Nemeth, D., & Janacsek, K. (2019). Is there more room to improve? The lifespan trajectory of procedural learning and its relationship to the between-and within-group differences in average response times. *PloS one, 14*(7), e0215116.

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language, 127*(1), 46-54.

Kim, H. (2010). Dissociating the roles of the default-mode, dorsal, and ventral networks in episodic memory retrieval. *Neuroimage, 50*(4), 1648-1657.

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: is it long-term and implicit? *Neuroscience Letters, 461*(2), 145-149.

King, B. R., Hoedlmoser, K., Hirschauer, F., Dolfen, N., & Albouy, G. (2017). Sleeping on the motor engram: the multifaceted nature of sleep-related motor memory consolidation. *Neuroscience & Biobehavioral Reviews, 80*, 1-22.

Kóbor, A., Janacsek, K., Takács, Á., & Nemeth, D. (2017). Statistical learning leads to persistent memory: Evidence for one-year consolidation. *Scientific Reports, 7*(1), 760.

Kóbor, A., Takács, Á., Kardos, Z., Janacsek, K., Csépe, V., & Nemeth, D. (2018). ERPs differentiate the sensitivity to statistical probabilities and the learning of sequential structures during procedural learning. *Biological Psychology, 135*, 180-193.

Manenti, R., Cotelli, M., Calabria, M., Maioli, C., & Miniussi, C. (2010). The role of the dorsolateral prefrontal cortex in retrieval from long-term memory depends on strategies: a repetitive transcranial magnetic stimulation study. *Neuroscience, 166*(2), 501-507.

Meier, B., & Cock, J. (2014). Offline consolidation in implicit sequence learning. *Cortex, 57*, 156-166.

Nagy, M., Kónya, A., & Király, I. (2013). Az Asszociatív Emlékezet Fejlődése 6–10 Éves Kor És Fiatal Felnőttkor Között. *Pszichológia, 33*(3), 169-184.

Naismith, S. L., Lagopoulos, J., Ward, P. B., Davey, C. G., Little, C., & Hickie, I. B. (2010). Fronto-striatal correlates of impaired implicit sequence learning in major depression: an fMRI study. *Journal of Affective Disorders, 125*(1-3), 256-261.

Nemeth, D., & Janacsek, K. (2011). The dynamics of implicit skill consolidation in young and elderly adults. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 66*(1), 15-22.

Nemeth, D., Janacsek, K., Csifcsak, G., Szvoboda, G., Howard Jr, J. H., & Howard, D. V. (2011). Interference between sentence processing and probabilistic implicit sequence learning. *PloS One, 6*(3), e17577.

Nemeth, D., Janacsek, K., & Fiser, J. (2013a). Age-dependent and coordinated shift in performance between implicit and explicit skill learning. *Frontiers in Computational Neuroscience, 7*, 147.

Nemeth, D., Janacsek, K., Londe, Z., Ullman, M. T., Howard, D. V., & Howard, J. H. (2010). Sleep has no critical role in implicit motor sequence learning in young and old adults. *Experimental Brain Research, 201*, 351-358.

Nemeth, D., Janacsek, K., Polner, B., & Kovacs, Z. A. (2013b). Boosting human learning by hypnosis. *Cerebral Cortex, 23*(4), 801-805.

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19*(1), 1-32.

Obeid, R., Brooks, P. J., Powers, K. L., Gillespie-Lynch, K., & Lum, J. A. (2016). Statistical learning in specific language impairment and autism spectrum disorder: A meta-analysis. *Frontiers in Psychology, 7*, 1245.

Oehrn, C. R., Fell, J., Baumann, C., Rosburg, T., Ludowig, E., Kessler, H., Hanslmayr, S., & Axmacher, N. (2018). Direct electrophysiological evidence for prefrontal control of hippocampal processing during voluntary forgetting. Current Biology, 28(18), 3016-3022.

Papagno, C., & Trojano, L. (2018). Cognitive and behavioral disorders in Parkinson's disease: an update. I: cognitive impairments. *Neurological Sciences, 39*(2), 215-223.

Park, J., Janacsek, K., Nemeth, D., & Jeon, H. A. (2022). Reduced functional connectivity supports statistical learning of temporally distributed regularities. *NeuroImage, 260*, 119459.

Parks, K. M. A., Griffith, L. A., Armstrong, N. B., & Stevenson, R. A. (2020). Statistical learning and social competency: The mediating role of language. *Scientific Reports 10*(1), 3968.

Pascual-Leone, A., Gates, J. R., & Dhuna, A. (1991). Induction of speech arrest and counting errors with rapid-rate transcranial magnetic stimulation. *Neurology, 41*(5), 697-702.

Pascual-Leone, A., Wassermann, E. M., Grafman, J., & Hallett, M. (1996). The role of the dorsolateral prefrontal cortex in implicit procedural learning. *Experimental Brain Research*, 107, 479-485.

Pedraza, F., Vékony, T., & Nemeth, D. (2023). Nomen est omen: Serial reaction time task is not a motor but a visuomotor learning task. *European Journal of Neuroscience, 58*(4), 3111-3115.

Peigneux, P., Laureys, S., Fuchs, S., Destrebecqz, A., Collette, F., Delbeuck, X., Phillips, C., Aerts, J., Del-Fiore, G., Degueldre, C., Luxen, A., Cleeremans, A., & Maquet, P. (2003). Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *Neuroimage, 20*(1), 125-134.

Peigneux, P., Orban, P., Balteau, E., Degueldre, C., Luxen, A., Laureys, S., & Maquet, P. (2006). Offline persistence of memory-related cerebral activity during active wakefulness. *PLoS biology, 4*(4), e100.

Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: One phenomenon, two approaches. *Trends in Cognitive Sciences, 10*(5), 233-238.

Polanía, R., Nitsche, M. A., & Ruff, C. C. (2018). Studying and modifying brain function with non-invasive brain stimulation. *Nature Neuroscience, 21*(2), 174-187.

Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia, 41*(3), 245-251.

Prashad, S., Du, Y., & Clark, J. E. (2021). Sequence structure has a differential effect on underlying motor learning processes. *Journal of Motor Learning and Development, 9*(1), 38-57.

Quentin, R., Fanuel, L., Kiss, M., Vernet, M., Vékony, T., Janacsek, K., Cohen, L. G., & Nemeth, D. (2021). Statistical learning occurs during practice while high-order rule learning during rest period. *NPJ Science of Learning, 6*(1), 14.

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior, 6*(6), 855–863.

Reber, P. J. (2013). The neural basis of implicit learning and memory: a review of neuropsychological and neuroimaging research. *Neuropsychologia, 51*(10), 2026-2042.

Robertson, E. M. (2007). The serial reaction time task: implicit motor skill learning? *Journal of Neuroscience, 27*(38), 10073-10075.

Robertson, E. M. (2009). From creation to consolidation: a novel framework for memory processing. *PLoS biology, 7*(1), e1000019.

Robertson, E. M., Pascual-Leone, A., & Press, D. Z. (2004). Awareness modifies the skill-learning benefits of sleep. *Current Biology, 14*(3), 208-212.

Robertson, E. M., Press, D. Z., & Pascual-Leone, A. (2005). Off-line learning and the primary motor cortex. *Journal of Neuroscience, 25*(27), 6372-6378.

Robertson, E. M., Tormos, J. M., Maeda, F., & Pascual-Leone, A. (2001). The role of the dorsolateral prefrontal cortex during sequence learning is specific for spatial information. *Cerebral Cortex, 11*(7), 628-635.

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996a). Statistical learning by 8-month-old infants. *Science, 274*(5294), 1926–1928.

Saffran, J. R., Newport, E. L., & Aslin, R. N. (1996b). Word segmentation: The role of distributional cues. *Journal of Memory and Language, 35*(4), 606-621.

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience, 26*(8), 1736-1747.

Schapiro, A. C., Kustner, L. V., & Turk-Browne, N. B. (2012). Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Current Biology, 22*(17), 1622-1627.

Schapiro, A. C., Turk-Browne, N. B., Botvinick, M. M., & Norman, K. A. (2017). Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1711), 20160049.

Schuck, N. W., & Niv, Y. (2019). Sequential replay of nonspatial task states in the human hippocampus. *Science, 364*(6447), eaaw5181.

Shaqiri, A., Anderson, B., & Danckert, J. (2013). Statistical learning as a tool for rehabilitation in spatial neglect. *Frontiers in Human Neuroscience, 7*, 224.

Shen, Q. R., Hu, M. T., Feng, W., Li, K. P., & Wang, W. (2022). Narrative review of noninvasive brain stimulation in stroke rehabilitation. *Medical Science Monitor: International Medical Journal of Experimental and Clinical Research, 28*, e938298-1.

Sherman, B. E., Graves, K. N., & Turk-Browne, N. B. (2020). The prevalence and importance of statistical learning in human cognition and behavior. *Current Opinion in Behavioral Sciences, 32*, 15-20.

Sherman, B. E., Turk-Browne, N. B., & Goldfarb, E. V. (2024). Multiple memory subsystems: Reconsidering memory in the mind and brain. *Perspectives on Psychological Science, 19*(1), 103-125.

Siegelman, N., Bogaerts, L., & Frost, R. (2017). Measuring individual differences in statistical learning: Current pitfalls and possible solutions. *Behavior Research Methods, 49*, 418-432.

Simor, P., Zavecz, Z., Horváth, K., Éltető, N., Török, C., Pesthy, O., Gombos, F., Janacsek, K., & Nemeth, D. (2019). Deconstructing procedural memory: Different learning trajectories and consolidation of sequence and statistical learning. *Frontiers in Psychology, 9*, 2708.

Smalle, E. H., Daikoku, T., Szmalec, A., Duyck, W., & Möttönen, R. (2022). Unlocking adults' implicit statistical learning by cognitive depletion. *Proceedings of the National Academy of Sciences, 119*(2), e2026011119.

Smalle, E. H., & Möttönen, R. (2023). Cognitive development as a piece of the language learning puzzle. *Cognitive Science, 47*(5), e13296.

Smalle, E. H., Panouilleres, M., Szmalec, A., & Möttönen, R. (2017). Language learning in the adult brain: Disrupting the dorsolateral prefrontal cortex facilitates word-form learning. *Scientific Reports, 7*(1), 13966.

Song, S., Howard, J. H., & Howard, D. V. (2007). Sleep does not benefit probabilistic motor sequence learning. *Journal of Neuroscience, 27*(46), 12475-12483.

Squire, L. R. (2004). Memory systems of the brain: a brief history and current perspective. *Neurobiology of Learning and Memory, 82*(3), 171-177.

Squire, L. R., Genzel, L., Wixted, J. T., & Morris, R. G. (2015). Memory consolidation. *Cold Spring Harbor Perspectives in Biology, 7*(8), a021766.

Stark-Inbar, A., Raza, M., Taylor, J. A., & Ivry, R. B. (2017). Individual differences in implicit motor learning: task specificity in sensorimotor adaptation and sequence learning. *Journal of Neurophysiology, 117*(1), 412-428.

Szegedi-Hallgató, E., Janacsek, K., & Nemeth, D. (2019). Different levels of statistical learning-hidden potentials of sequence learning tasks. PloS one, 14(9), e0221966.

Szegedi-Hallgató, E., Janacsek, K., Vékony, T., Tasi, L. A., Kerepes, L., Hompoth, E. A., Bálint, A., & Németh, D. (2017). Explicit instructions and consolidation promote rewiring of automatic behaviors in the human mind. *Scientific Reports, 7*(1), 4365.

Szücs-Bencze, L., Vékony, T., Pesthy, O., Szabó, N., Kincses, T. Z., Turi, Z., & Nemeth, D. (2023). Modulating visuomotor sequence learning by repetitive transcranial magnetic stimulation: what do we know so far? *Journal of Intelligence, 11*(10), 201.

Toro, J. M., Sinnett, S., & Soto-Faraco, S. (2005). Speech segmentation by statistical learning depends on attention. *Cognition, 97*(2), B25-B34.

Tóth, B., Janacsek, K., Takács, Á., Kóbor, A., Zavecz, Z., & Nemeth, D. (2017). Dynamics of EEG functional connectivity during statistical learning. *Neurobiology of Learning and Memory*, 144, 216-229.

Tóth-Fáber, E., Janacsek, K., Szőllősi, Á., Kéri, S., & Nemeth, D. (2021a). Regularity detection under stress: Faster extraction of probability-based regularities. *Plos one, 16*(6), e0253123.

Tóth-Fáber, E., Nemeth, D., & Janacsek, K. (2023). Lifespan developmental invariance in memory consolidation: evidence from procedural memory. *PNAS nexus, 2*(3), pgad037.

Tóth-Fáber, E., Tárnok, Z., Janacsek, K., Kóbor, A., Nagy, P., Farkas, B. C., Oláh, Sz., Merkl, D., Hegedűs, O., Nemeth, D., & Takács, Á. (2021b). Dissociation between two aspects of procedural learning in Tourette syndrome: Enhanced statistical and impaired sequence learning. *Child Neuropsychology, 27*(6) 799-821.

Tunovic, S., Press, D. Z., & Robertson, E. M. (2014). A physiological signal that prevents motor skill improvements during consolidation. *Journal of Neuroscience, 34*(15), 5302-5310.

Turi, Z., Hananeia, N., Shirinpour, S., Opitz, A., Jedlicka, P., & Vlachos, A. (2022). Dosing transcranial magnetic stimulation of the primary motor and dorsolateral prefrontal cortices with multi-scale modeling. *Frontiers in Neuroscience, 16*, 929814.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General, 134*(4), 552.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: Efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience, 21*(10), 1934-1945.

Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition, 92*(1-2), 231-270.

Veldman, M. P., Maurits, N. M., Nijland, M. A. M., Wolters, N. E., Mizelle, J. C., & Hortobágyi, T. (2018). Spectral and temporal electroencephalography measures reveal distinct neural networks for the acquisition, consolidation, and interlimb transfer of motor skills in healthy young adults. *Clinical Neurophysiology, 129*(2), 419-430.

Vékony, T., Pleche, C., Pesthy, O., Janacsek, K., & Nemeth, D. (2022). Speed and accuracy instructions affect two aspects of skill learning differently. npj Science of Learning, 7(1), 27.

Vékony, T., Török, L., Pedraza, F., Schipper, K., Pleche, C., Tóth, L., Janacsek, K., & Nemeth, D. (2020). Retrieval of a well-established skill is resistant to distraction: Evidence from an implicit probabilistic sequence learning task. *PloS one, 15*(12), e0243541.

Virag, M., Janacsek, K., Horvath, A., Bujdoso, Z., Fabo, D., & Nemeth, D. (2015). Competition between frontal lobe functions and implicit sequence learning: evidence from the long-term effects of alcohol. *Experimental Brain Research, 233*, 2081-2089.

Walker, M. P., & Stickgold, R. (2004). Sleep-dependent learning and memory consolidation. *Neuron, 44*(1), 121-133.

Wassermann, E. M., McShane, L. M., Hallett, M., & Cohen, L. G. (1992). Noninvasive mapping of muscle representations in human motor cortex. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 85*(1), 1-8.

Wessel, M. J., Zimerman, M., & Hummel, F. C. (2015). Non-invasive brain stimulation: an interventional tool for enhancing behavioral training after stroke. *Frontiers in Human Neuroscience, 9*, 265.

Wilkinson, L., Khan, Z., & Jahanshahi, M. (2009). The role of the basal ganglia and its cortical connections in sequence learning: evidence from implicit and explicit sequence learning in Parkinson's disease. *Neuropsychologia, 47*(12), 2564-2573.

Wilkinson, L., Steel, A., Mooshagian, E., Zimmermann, T., Keisler, A., Lewis, J. D., & Wassermann, E. M. (2015). Online feedback enhances early consolidation of motor sequence learning and reverses recall deficit from transcranial stimulation of motor cortex. *Cortex, 71*, 134-147.

Woodcock, E. A., White, R., & Diwadkar, V. A. (2015). The dorsal prefrontal and dorsal anterior cingulate cortices exert complementary network signatures during encoding and retrieval in associative memory. *Behavioural Brain Research, 290*, 152-160.

Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., & Grafton, S. T. (2012). Differential recruitment of the sensorimotor putamen and frontoparietal cortex during motor chunking in humans. *Neuron, 74*(5), 936-946.

I.

Supplementary Materials

Enhancing Retrieval Capacity of the Predictive Brain through Dorsolateral Prefrontal Cortex Intervention

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Declaration of interests

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Supplementary Table 1. Results of model comparison of the Learning session

Model	Description	k	AIC	log-likelihood
M1	FE(Group × Block × Trial Type) + RE(1|Subject)	18	44951	-22458
M2	**FE(Group × Block × Trial Type) + RE(Block|Subject)**	20	**44497**	-22228
M3	FE(Block × Trial Type) + RE(1|Subject)	6	44992	-22490
M4	FE(Block × Trial Type) + RE(Block|Subject)	8	44505	-22244
M5	FE(Group × Trial Type) + RE(1|Subject)	10	46873	-23426
M6	FE(Group × Trial Type) + RE(Block|Subject)	12	44671	-22324

FE = fixed effects, RE = random effects, k = number of parameters, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion

Supplementary Table 2. Linear mixed model analysis of mean RTs of the Learning session

Fixed effects	*b*	*SE b*	*95% CI*	*t*	*p*
(Intercept)	359.62	3.97	[351.83, 367.41]	90.52	< .001
Bilateral DLPFC	0.67	6.90	[-12.86, 14.20]	0.09	.92
Left DLPFC	1.57	6.90	[-11.95, 15.11]	0.22	.81
Right DLPFC	0.08	6.90	[-13.44, -13.61]	0.01	.99
Block	-13.26	0.73	[-14.71, -11.81]	-17.93	< .001
Trial Type	-4.32	0.25	[-4.83, -3.81]	-16.69	< .001
Bilateral DLPFC × Block	1.91	1.28	[-0.60, 4.43]	1.49	.13
Left DLPFC × Block	-2.67	1.28	[-5.19, -0.15]	-2.08	.03
Right DLPFC × Block	-0.77	1.28	[-3.29, 1.74]	-0.60	.54
Bilateral DLPFC × Trial Type	0.34	0.45	[-0.53, 1.23]	0.77	.44
Left DLPFC × Trial Type	-0.35	0.45	[-1.23, 0.53]	-0.78	.43
Right DLPFC × Trial Type	0.24	0.45	[-0.63, 1.13]	0.55	.58
Block × Trial Type	-1.50	0.25	[-2.01, -0.99]	-5.79	< .001
Bilateral DLPFC × Block × Trial Type	0.05	0.45	[-0.82, 0.93]	0.12	.90
Left DLPFC × Block × Trial Type	0.34	0.45	[-0.53, 1.22]	0.76	.44
Right DLPFC × Block × Trial Type	-0.04	0.45	[-0.92, 0.83]	-0.10	.91
Random effects					
σ^2	338.86				
$\tau00_{\text{Subject}}$	1586.93				
$\tau11_{\text{Subject.Block}}$	48.42				
$\rho01_{\text{Subject}}$	-0.38				
ICC	0.83				
N_{Subject}	101				
Observations	5050				
Marginal R^2/Conditional R^2	0.93/0.84				

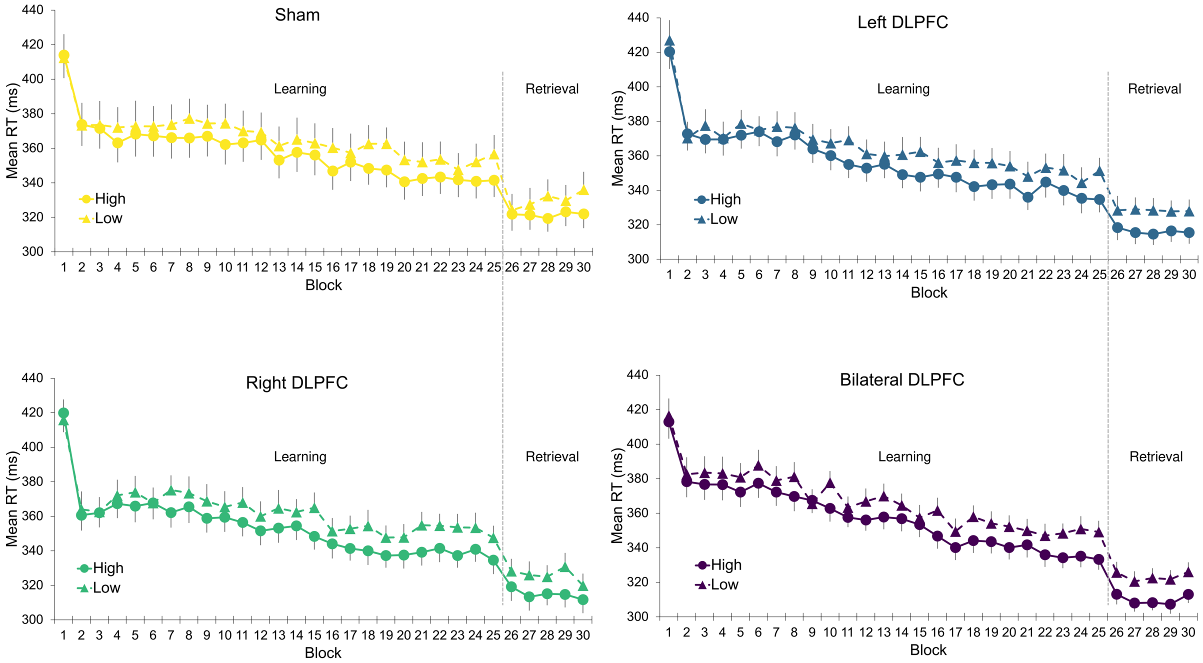
Supplementary Table 3. Results of model comparison of the Retrieval session

Model	Description	k	AIC	log-likelihood
M1	FE(Group × Block × Trial Type) + RE(1|Subject)	18	8455.6	-4209.8
M2	FE(Group × Block × Trial Type) + RE(Block|Subject)	20	8419.2	-4189.6
M3	FE(Block × Trial Type) + RE(1|Subject)	6	8477.2	-4232.6
M4	FE(Block × Trial Type) + RE(Block|Subject)	8	8438.6	-4211.3
M5	FE(Group × Trial Type) + RE(1|Subject)	10	8457.7	-4218.9
M6	**FE(Group × Trial Type) + RE(Block|Subject)**	**12**	**8418.4**	-4197.2

FE = fixed effects, RE = random effects, k = number of parameters, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion

Supplementary Table 4. Linear mixed model analysis of mean RTs of the Retrieval session

Fixed effects	*b*	*SE b*	*95% CI*	*t*	*p*
(Intercept)	319.02	3.06	[313.00, 325.04]	104.03	< .001
Bilateral DLPFC	5.34	5.32	[-5.11, 15.80]	1.00	.31
Left DLPFC	-3.51	5.32	[-13.97, 6.93]	-0.66	.50
Right DLPFC	0.71	5.32	[-9.74, 11.17]	-0.13	.89
Trial Type	-5.41	0.38	[-6.16, -4.66]	-14.11	< .001
Bilateral DLPFC × Trial Type	2.01	0.66	[0.70, 3.32]	3.02	.003
Left DLPFC × Trial Type	-1.26	0.66	[-2.57, 0.04]	-1.89	.058
Right DLPFC × Trial Type	-0.88	0.66	[-2.19, 0.42]	-1.32	.18
Random effects					
σ^2	148.73				
$\tau00_{\text{Subject}}$	967.99				
$\tau11_{\text{Subject.Block}}$	19.88				
$\rho01_{\text{Subject}}$	-0.25				
ICC	0.87				
N_{Subject}	101				
Observations	1010				
Marginal R^2/Conditional R^2	0.03/0.87				



Supplementary Figure 1. Mean reaction times (RTs) of high-probability triplets (solid line with circle) and low-probability triplets (dashed line with triangle) are presented on the y-axis across all blocks (x-axis). A greater difference between the two triplet types indicates better statistical learning performance. Blocks 1-25 represent the Learning session, while Blocks 26-30 correspond to the Retrieval session. The performance of the four groups is shown with different colors. Error bars denote the standard error of the mean (SEM).

II.

Supplementary Materials

Manipulating the rapid consolidation periods in a learning task affects general skills more than statistical learning and changes the dynamics of learning

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Process Dissociation Procedures Task

Structure of the task

To determine whether learning of statistical regularities occurred implicitly, we administered a task based on the Process Dissociation Procedures (Jacoby, 1991), which is a widely used method to disentangle the explicit–implicit processes in memory tasks (Destrebecqz et al., 2005; Destrebecqz and Cleeremans, 2001; Fu et al., 2010; Jiménez et al., 2006). In the first part of the task, we asked participants to try to produce a sequence using the same four response keys used during the ASRT task (inclusion instruction). After that, we asked participants to try to generate new sequences that were different from the learned sequence (exclusion condition). Both parts consisted of four runs, and each run lasted up to 24 button presses, equal to 3 rounds of the eight-element alternating sequence (Horváth et al., 2020; Kóbor et al., 2017). Participants were instructed to create sequences that could have been used in the task (i.e., sequences that are not entirely repetitive). Accordingly, they were asked to avoid including repetitions (repeating key presses such as 3-3-3) or trills (alternating key presses such as 1-2-1) in their answers as much as possible. The reason was that producing repeating or alternating key presses could be a strategy to create a sequence that was not used during the task (exclusion condition) since long repetitions and alternations did not occur during the task. This strategy can be used to create sequences that match the exclusion instruction but contain only low-probability triplets (because repetitions and trills are always the last elements of low-probability triplets), which makes implicit estimation inefficient. The runs where more than 50% of participants' key presses were either repetitions or trills were removed from the analysis. As a result, seven participants from the self-paced group, 3 participants from the 15-sec group, and 3 participants from the 30-sec group were removed entirely from the analysis, as their answers only contained trills and repetitions in the exclusion condition.

We assessed the implicitness of the participants' knowledge by calculating the ratio of high-probability triplets in the sequence of responses. The chance level of generating high-probability triplets was considered 25% because, after two consecutive button presses, the chance for the third button press to form a high-probability triplet with the two preceding button presses is 1/4 = 25%. We also compared the percentages of the high-probability triplets across conditions (inclusion and exclusion condition) and groups (self-paced, 15-sec, 30-sec).

If the ratio of high-probability triplets is above the chance level in the inclusion condition, we can conclude that participants successfully learned the sequence. Although the above-chance level ratio of high-probability triplets in the inclusion condition can be achieved solely by implicit knowledge, explicit knowledge can also boost performance. On the contrary, above-chance level ratio of high-probability triplets in the exclusion condition (i.e., when trying to generate a new sequence that is different from the learned one) indicates that the participant relies on their implicit knowledge, as it cannot be controlled consciously.

Results

First, we compared the percentage of the high-probability triplets to the chance level (25%) separately for the three groups. Participants in the self-paced group generated 31.5% ± 0.8 SD high-probability triplets in the inclusion condition, significantly higher than the chance level, $t(80) = 7.79$, $p < .001$, $BF_{01} = 0.001$. In the exclusion condition, they generated 29.2% ± 1 SD high-probability triplets, which is significantly above the chance level, $t(80) = 3.06$, $p < .001$, $BF_{01} < 0.001$. In the 15-sec group, participants generated 31.1% ± 0.8 SD high-probability triplets in the inclusion condition, significantly above the chance level, $t(86) = 7.54$, $p = .001$, $BF_{01} < 0.001$. They also generated more high-probability triplets than expected by chance in the exclusion condition, 27.5% ± 1 SD, $t(80) = 2.62$, $p = .001$, $BF_{01} < 0.001$. In the 30-sec group, participants generated 30.3% ± 0.7 SD high-probability triplets in the inclusion condition, significantly above the chance level, $t(86) = 6.57$, $p < .001$,

$BF_{01} < 0.001$. They also generated more high-probability triplets than expected by chance in the exclusion condition, 29.0% ± 1 SD, $t(80) = 3.30$, $p = .001$, $BF_{01} < 0.001$. Thus, we can conclude that in all groups, the learning is deemed to be implicit.

Furthermore, we explored the potential differences between groups with a two (condition: inclusion vs. exclusion) × three (group: self-paced vs. 15-sec vs. 30-sec) ANOVA. The main effect of the condition was significant, $F(1, 252) = 15.027$, $p = .001$, $\eta_p^2 = .06$, $BF_{\text{exclusion}} = 0.01$, indicating that participants performed better in the inclusion condition. The group main effect did not reach significance, $F(2, 252) = 0.13$, $p = .88$, $\eta_p^2 = .001$, $BF_{\text{exclusion}} = 28.02$, indicating that the three groups performed equally on the tasks. The interaction of the condition and group factors were also not significant, $F(2, 252) = 1.03$, $p = 0.36$, $\eta_p^2 = 0.01$, $BF_{\text{exclusion}} = 9.35$, revealing that the lack of difference between groups was not influenced by the task condition. Taken together, the results indicate that the knowledge of the three groups was equally implicit.

Results without age-based exclusion

We have excluded 11 participants from the main analyses to equalize the mean age between groups in order to ensure that age-related differences have no effect on our results. Here, we present the results including the participants that were excluded based on their age.

Results of statistical learning

To test whether the duration of rest periods between learning blocks affected statistical learning, we conducted a mixed-design ANOVA with the within-subjects factor of Blocks (Blocks 1-5 vs. Blocks 6-10 vs. Blocks 11-15 vs. Blocks 16-20 vs. Blocks 21-25) and the between-subjects factor of Group (self-paced, 15-sec breaks, 30-sec breaks) on the learning scores. The analyses revealed a gradual increase of learning scores in each group, irrespective of the rest period duration [main effect of Blocks, $F(4, 1104) = 25.00$, $p < .001$, $\eta_p^2 = .08$, $BF_{\text{exclusion}} < 0.001$]. According to pairwise comparisons, there was no significant increase in learning between Blocks 6-10 and Blocks 11-15 ($p = .61$), between Blocks 6-10 and Blocks 16-20 ($p = .07$), between Blocks 11-15 and Blocks 16-20 ($p < .99$), and between Blocks 16-20 and Blocks 21-25 ($p = .12$). All other paired comparisons of block arrays were significant (all $p < .01$). Thus, the consecutive learning units did not significantly differ from each other, learning could be discovered between temporally more distant parts of the task. Importantly, the three experimental groups did not differ in statistical learning [main effect of Group, $F(2, 276) = 0.32$, $p = .73$, $\eta_p^2 < .01$, $BF_{\text{exclusion}} = 64.46$. The Blocks × Group interaction was also non-significant, $F(8, 1104) = 0.28$, $p = .97$, $\eta_p^2 < .01$, $BF_{\text{exclusion}} = 40\ 229.19$, thus the three groups did not differ in the time course of statistical learning either.

Results of general skill learning

To test whether the overall speed-up on the task differed between groups (i.e., whether the duration of rest periods between learning blocks affected general skill learning), we conducted a mixed-design ANOVA with the within-subjects factor of Blocks (Blocks 1-5 vs.

Blocks 6-10 vs. Blocks 11-15 vs. Blocks 16-20 vs. Blocks 21-25) and the between-subjects factor of Group (self-paced, 15-sec breaks, 30-sec breaks) with median RT as the dependent variable. We found a gradual decrease in RTs throughout the task [main effect of Blocks, $F(2.76, 760.79) = 290.75$, $p < .001$, $\eta_p^2 = .51$, $BF_{\text{exclusion}} < 0.001$]. Based on pairwise comparisons, every epoch significantly differed from each other (all $p < .01$), with increasing learning through all blocks. The three groups significantly differed in response times [main effect of Group, $F(2, 276) = 9.77$, $p < .001$, $\eta_p^2 = .07$, $BF_{\text{exclusion}} = 0.01$], with the self-paced group being slower than the 15-sec and 30-sec groups. The Blocks × Group interaction was also significant, $F(8, 1104) = 2.36$, $p = .04$, $\eta_p^2 = .02$, $BF_{\text{exclusion}} = 1.18$]. Pairwise comparisons revealed significantly higher RTs in the self-paced compared to the 30-sec group in Blocks 6-10, Blocks 11-15, Blocks 16-20 and Blocks 21-25 (all $p < .01$). The self-paced group also showed significantly higher RTs compared to the 15-sec group in Blocks 6-10, Blocks 11-15, Blocks 16-20, and Blocks 21-25 (all $p < .01$). Thus, the three groups showed a similar speed in the first learning unit, but the self-paced group began to slow down compared to the other two groups starting from the second learning unit.

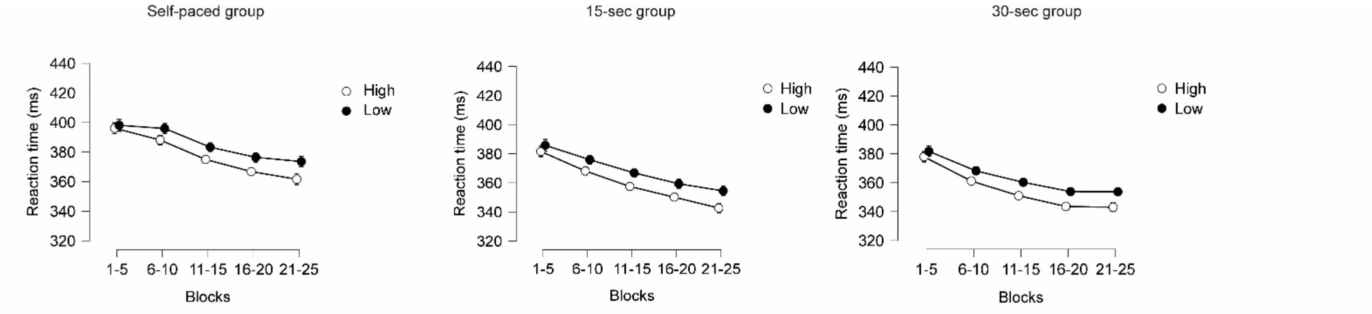
Results of offline vs. online learning

We ran a mixed design ANOVA with the within-subjects factor of Learning Phase (offline vs. online) and the between-subject factor of Group (self-paced, 15-sec breaks, 30-sec breaks) on the change scores of statistical learning. The ANOVA revealed an interaction between Learning Phase and Group factors, $F(2, 276) = 3.17$, $p = .04$, $\eta_p^2 = .02$, $BF_{\text{exclusion}} = 0.09$. Bonferroni-corrected post-hoc comparisons revealed that online and offline changes differed in the 15-sec break group ($p = .04$): the offline changes were significantly smaller than the online changes. No main effect of Group [$F(2, 276) = 1.09$, $p = .34$, $\eta_p^2 = .01$, $BF_{\text{exclusion}} = 45.90$] or Learning Phase was found [$F(2, 276) = 3.51$, $p = .06$, $\eta_p^2 = .01$, $BF_{\text{exclusion}} = 0.44$].

We ran a mixed design ANOVA on the change scores of general skill learning, with the within-subjects factor of Learning Phase (offline vs. online) and the between-subject factor of Group (self-paced, 15-sec breaks, 30-sec breaks). We found the main effect of Learning Phase [$F(2, 276) = 645.95$, $p < .001$, $\eta_p^2 = 0.70$, $BF_{\text{exclusion}} < 0.001$], with a slowing down of RT during the blocks, while an acceleration of RTs occurred after the rests. No main effect of Group was found [$F(2, 276) = 0.17$, $p = .85$, $\eta_p^2 < .001$, $BF_{\text{exclusion}} = 45.35$]. The interaction between the Learning Phase and Group factors were significant [$F(2, 276) = 3.75$, $p = .03$, $\eta_p^2 = .03$, $BF_{\text{exclusion}} = 0.03$]. However, no differences survived Bonferroni-corrected between-group comparisons for online and offline changes (all comparisons between groups revealed $p > .17$).

Performance of high- and low-probability triplets in the three groups

In the Supplementary Figure 1, we depicted the original high- and low-probability triplet variables can in each group.



Supplementary Figure 1. *Performance of high-probability (empty circles) and low-probability (filled circles) triplets in the three groups. The y-axes indicates the median RT. The x-axes shows the blocks grouped by five. The error bars represent 95% confidence interval.*

Offline and online changes in statistical learning across all blocks

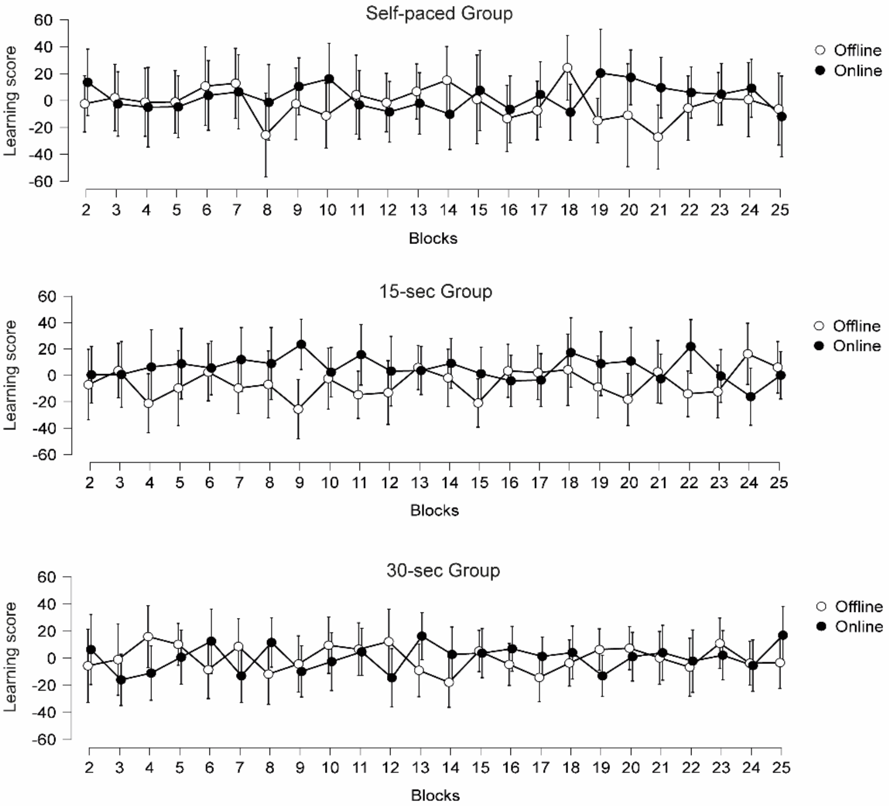
To see how offline and online statistical learning dynamically change across all blocks in the separate groups, we conducted three ANOVAs with the offline and online statistical learning scores of all blocks separately for each group.

In the self-paced group, there was not significant neither the main effect of Blocks ($F(10.56, 401.26) = 0.85$, $p = .59$, $\eta_p^2 = .02$), nor the main effect of Learning Phase ($F(1, 38) = 0.88$, $p = .35$, $\eta_p^2 = .02$). The Blocks × Learning Phase interaction was also not significant ($F(12.82, 487.30) = 0.69$, $p = .77$, $\eta_p^2 = .02$).

In the 15-sec group, the main effect of Blocks was also not significant ($F(9.98, 468.87) = 0.46$, $p = .92$, $\eta_p^2 = .01$). The main effect of Learning Phase was significant only in this group ($F(1, 47) = 7.57$, $p < .01$, $\eta_p^2 = .14$). However, the Blocks × Learning Phase interaction was not significant $F(13.71, 644.47) = 0.97$, $p = .48$, $\eta_p^2 = .02$).

In the 30-sec group, there was not significant neither the main effect of Blocks ($F(10.82, 486.66) = 0.77$, $p = .67$, $\eta_p^2 = .02$), nor the main effect of Learning Phase ($F(1, 45) = 0.01$, $p = .94$, $\eta_p^2 < .001$). The Blocks × Learning Phase interaction was also not significant ($F(13.51, 607.93) = 1.02$, $p = .43$, $\eta_p^2 = .02$).

We also depict the dynamic change of offline and online statistical learning across all blocks in the different groups. We can see in the Supplementary Figure 2 that the 15-sec group is the only one where online learning scores are consistently higher than offline learning scores throughout the task, which is also supported by the results of the ANOVA.



Supplementary Figure 2. *Dynamic change of offline and online learning scores across the 24 blocks in each group. The y-axis indicates the mean learning score. The x-axis shows the blocks. The error bars represent 95% confidence interval.*

Dynamics of offline/online statistical learning and forgetting in the different groups

As offline and online statistical learning in the self-paced and 30-sec groups were not different from zero at a group level, we have checked whether there is a difference within the groups between the numbers of online and offline learning and forgetting scores. In Supplementary Table 1, we compared the distribution of those who had high positive (≤5) or high negative (≥-5) offline learning scores in the three groups.

Supplementary Table 1. The distribution of positive and negative offline learning scores in the groups

	Group			
	Self-paced	**15-sec**	**30-sec**	**Total**
Learn offline	38	25	27	90
Forget offline	31	49	34	114
Total	69	74	61	204

Chi-square test: $\chi^2(2) = 6.57$, $p < 0.05$

As we can see, the distribution of those who learned or forgot offline is in balance in the self-paced and the 30-sec group, which could be resulted in no offline learning at group level. However, in the 15-sec group, more participants forgot than learned offline, which resulted in offline forgetting at a group level. The chi-square test was significant ($\chi^2(2) = 6.57$, $p < 0.05$).

Distributions in high positive and high negative learning scores were also tested for online learning (see Supplementary Table 2). Similarly to offline learning, in the self-paced and the 30-sec group the proportion of those who learned or forgot online is similar, while in the 15-sec group, almost twice as many participants learned as forgot online. The chi-square test was significant at a trend level ($\chi^2(2) = 5.67$, $p = 0.06$).

Supplementary Table 2. The distribution of positive and negative online learning scores in the groups

	Group			
	Self-paced	**15-sec**	**30-sec**	**Total**
Learn online	34	50	34	118
Forget online	38	25	26	89
Total	72	75	60	207

Chi-square test: $\chi^2(2) = 5.67$, $p = 0.06$

References

Destrebecqz, A., and Cleeremans, A. (2001). Can sequence learning be implicit? New evidence with the process dissociation procedure. *Psychonomic Bulletin and Review*, *8*(2), 343–350. https://doi.org/10.3758/BF03196171

Destrebecqz, A., Peigneux, P., Laureys, S., Degueldre, C., Del Fiore, G., Aerts, J., Luxen, A., Van Der Linden, M., Cleermans, A., Maquet, P., Fiore, G. Del, Aerts, J., Luxen, A., Van Der Linden, M., Cleeremans, A., and Maquet, P. (2005). Neural correlates of implicit and explicit sequence learning: Interacting networks revealed. *Learning & Memory*, *12*(5), 480–490. https://doi.org/10.1101/lm.95605.6

Fu, Q., Dienes, Z., and Fu, X. (2010). Can unconscious knowledge allow control in sequence learning? *Consciousness and Cognition*, *19*(1), 462–474. https://doi.org/10.1016/j.concog.2009.10.001

Horváth, K., Török, C., Pesthy, O., Nemeth, D., and Janacsek, K. (2020). Divided attention does not affect the acquisition and consolidation of transitional probabilities. *Scientific Reports*, *10*(1), 1–14. https://doi.org/10.1038/s41598-020-79232-y

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, *30*(5), 513–541. https://doi.org/10.1016/0749-596X(91)90025-F

Jiménez, L., Vaquero, J. M. M., and Lupiáñez, J. (2006). Qualitative differences between implicit and explicit sequence learning. *Journal of Experimental Psychology: Learning Memory and Cognition*, *32*(3), 475–490. https://doi.org/10.1037/0278-7393.32.3.475

Kóbor, A., Janacsek, K., Takács, A., Nemeth, D., Kobor, A., Janacsek, K., Takacs, A., and Nemeth, D. (2017). Statistical learning leads to persistent memory: Evidence for one-year consolidation. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/s41598-017-00807-3