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The interplay between the procedural memory and executive control systems in behaviour adaptation

Doctoral dissertation

DOI identifier: 10.15476/ELTE.2022.265

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Budapest, 2022

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my first mentor, Dezső Németh, who has always supported me on my academic path as well as in my personal life. He showed me the fun and exciting sides of science, while at the same time providing a safety net so that I could explore my interests. He always had trust in me, and I will be for ever grateful for him.

Next, I would like to thank my supervisors, Karolina Janacsek and Andrea Kóbor. Both of them imparted an immense amount of theoretical and methodological knowledge, tirelessly pushed me to do my best, and showed me how to build a successful career in science as a woman. I consider myself extremely lucky to have worked with them. I owe a special thank you to Andrea Kóbor for all the time and energy she has dedicated to this dissertation.

I am thankful for all my other co-authors, especially those who I worked with on the papers included in this dissertation, namely Valéria Csépe, Zsófia Kardos, Orsolya Pesthy, Ádám Takács, and Csenge Török.

I am obliged to the past and present members of the Brain, Memory and Language Lab for all the support they have given me over the years. In particular, Eszter Tóth-Fáber and Zsófia Zavecz, who have always been ready to help, be it a challenging analysis, some paperwork, or everyday troubles. I owe many thanks to all who helped in data collection, particularly Ábel Gergely, Anna Guttengéber, Kristóf Mikó, Péter Solymosi, and Balázs Török. I would also like to thank the Neurocognitive Development Research Group for welcoming me as one of their own members, and to the Department of Cognitive Psychology at ELTE for being such a supportive and inspirational community.

During my PhD years, I was granted several scholarships from ELTE and the Hungarian government which had provided me opportunities to travel and gain experience in different fields of science as well as to participate in international conferences. I appreciate all of these.

I would like to express my great appreciation to Jonathan Webb who proofread this dissertation and many of my other works, and who has also provided me with patient guidance and support during this challenging period.

Finally, I would like to dedicate this dissertation to my father, who couldn't be there to defend his own work.

Table of Contents

ABBREVIATIONS

ASRT – Alternating Serial Reaction Time (task)

CSE – Congruency sequence effect

ERN – Error-related negativity (same as Ne)

ERP – Event-related brain potential

FDR – False discovery rate (correction)

Ne – Error negativity

Pe – Error positivity

PES – Post-error slowing

PFC – Prefrontal cortex

RT – Reaction time

ABSTRACT

Successful adaptation requires both automatic and goal-directed behaviours, and these often need to operate in parallel with one another. However, the nature of their interplay is yet to be fully unravelled: some studies suggest independent operation, whereas others propose an interactive relationship. Moreover, different lines of research have drawn different conclusions about the nature of the assumed interactive relationship. Through five studies (Study 1-4 and the Supplementary Study), I aimed to investigate how automatic and goal-directed behaviours *naturally* interact during behaviour adaptation in a reaction time task as well as when the engagement of goal-directed behaviours is *manipulated* during task solving. Automatic behaviours were modelled by the procedural memory system, whereas goal-directed behaviours were modelled by the components of the executive control system. Furthermore, I studied habit change, a challenging and complex aspect of behaviour adaption, which is closely related to procedural memory acquisition and expression. These studies provided cumulative evidence that procedural learning and memory expression are robust and take place independently of goal-directed behaviours. Importantly, when complex environmental and situational factors induced fragility in the procedural memory system, such as habit change or adaptation to interfering stimuli, a competing relationship emerged. Conversely, goal-directed behaviours seemed to operate independently of automatic behaviours, nevertheless, some evidence implied support for the executive control system from procedural learning. Overall, my doctoral research could shed light on the complex interplay behind adaptive behaviours in the ever-changing environment.

Keywords: automatic behaviours, behaviour adaptation, executive control system, goal-directed behaviours, habit change, procedural learning

List of studies that the dissertation is based upon

Study	Publication	Impact Factor
1	**Horváth, K.**, Kardos, Z., Takács, Á., Csépe, V., Nemeth, D., Janacsek, K., & Kóbor, A. (2021). Error processing during the online retrieval of probabilistic sequence knowledge. *Journal of Psychophysiology, 35*(2), 61-75. https://doi.org/10.1027/0269-8803/a000262	1.23
2	Kóbor, A., **Horváth, K.**, Kardos, Z., Nemeth, D., & Janacsek, K. (2020). Perceiving structure in unstructured stimuli: Implicitly acquired prior knowledge impacts the processing of unpredictable transitional probabilities. *Cognition*, *205*, 104413. https://doi.org/10.1016/j.cognition.2020.104413	3.65
3	**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), 1-14. https://doi.org/10.1038/s41598-020-79232-y	4.38
4	**Horváth, K.**, Nemeth, D., & Janacsek, K. (2022). Inhibitory control hinders habit change. *Scientific Reports*, *12*(1), 1-11. https://doi.org/10.1038/s41598-022-11971-6	5.00
Supplementary Study	**Horváth, K.**, Kardos, Z., Takács, Á., Nemeth, D., Janacsek, K., & Kóbor, A. Manipulation of inhibitory control does not influence procedural learning. *In preparation.*	-

GENERAL INTRODUCTION

I. Summary

Automatic and goal-directed actions are both essential in our everyday life. While our automatic behaviours allow us to act with little effort, goal-directed behaviours enable us to adjust our actions when required. By relying on both processes simultaneously, we can smoothly adapt our actions according to the requirements of the environment and our own goals. For example, when we take the same turn every day upon leaving our house to work absent-minded, we use our automatic behaviours. We don't need to pay attention to the route, and this frees our cognitive resources thus allowing us to focus on our to-do list for the day. Sometimes, of course, we need to take unknown routes. In these cases, we rely on our goal-directed behaviours: we need to keep in mind our new destination, inhibit turning in a wrong direction, and keep our attention on the new route. However, one day our usual morning commute to work might be disrupted by road works, hence we need to adjust our route. What happens in such a situation? Do our automatic and goal-directed behaviours operate independently, or do they interact with one another? If yes, do they support or compete with one another? Although examples like these are familiar to all of us, the exact neurocognitive background of the interplay between our automatic and goal-directed behaviours during behaviour adaptation is yet to be fully unravelled. My doctoral research aimed to better understand this interplay in healthy humans by investigating the interaction of the procedural memory system and the executive control system.

Automatic behaviours, such as habits and skills, at least partially rely on the procedural memory system (Ashby et al., 2010; Ullman, 2004). It enables us, through exposure, to process, extract, and acquire the probability-based structure organizing the noisy environment (Conway, 2020; Frost et al., 2019). This ability allows for the prediction of and adaptation to future events in the environment. Acquisition and memory expression in the procedural memory system are implicit, incidental, and automatic (Foerde, 2018; Graybiel, 2008; Jiménez & Mendez, 1999). The acquired automatic behaviours seem highly robust and resistant to forgetting and memory interference (Kóbor et al., 2017; Szegedi-Hallgató et al., 2017).

Goal-directed behaviours rely on a complex ensemble of various cognitive processes that operate in an orchestrated manner (Friedman & Robbins, 2022; Miller,

2000; Miyake et al., 2000). To successfully execute these behaviours, our brain needs to continuously monitor our performance and detect and process if we committed an erroneous action and so our behaviour is no longer optimal in the light of our goals. While doing so, focused and selective attention needs to be maintained to effectively process the goal-relevant information, and, if necessary, our attention might even have to be divided between several concurrent tasks or goals. In addition, our brain needs to inhibit actions that are irrelevant or even harmful for good performance as well as any distracting and irrelevant information from the environment. In case we slip and our performance drops, we need to correct our behaviour by updating our goals, selecting a new plan, and shifting our attention and behaviour according to the new plans (Bari & Robbins, 2013). In this dissertation, I refer to this ensemble of cognitive processes as the "executive control system", based on the different terms appearing in the related literature (e.g., executive functions, cognitive control, executive control processes).

Procedural memory and the executive control system frequently need to operate simultaneously during behaviour adaptation. Contrary, previous research investigating these behaviours often ignored one another and the literature remained mostly separated. The nature of the procedural memory vs. executive control system interaction received less attention and the effort towards clarifying this issue has led to inconsistent findings. Some studies suggest a cooperative/supportive interaction (Coomans et al., 2011; Deroost et al., 2012), some found evidence for competition/interference (Borragán et al., 2016; Nemeth, Janacsek, Polner, et al., 2013; Poldrack & Packard, 2003; Vaquero et al., 2020), whereas others proposed an independent relationship (Jiménez, Abrahamse, et al., 2020; Jiménez, Méndez, et al., 2020) between the two systems. This inconsistency might originate from the wide array of processes contributing to our automatic and goal-directed behaviours, the partial focus on only some of these processes, the lack of systematic investigation of their relationship, and the variety of the experimental tasks and designs. Furthermore, most studies focused on only the acquisition phase of procedural learning and neglected further steps, notably, the short(er) and long(er) term retention of the acquired behaviour. I aimed to consider the different aspects and phases of the procedural memory system as well as the different subcomponents of the executive control system in newly designed experiments. Thereby, the findings presented in the dissertation might contribute to a better understanding of whether and how these systems interact.

Recently, the world has faced major environmental threats, such as climate change and the Covid-19 pandemic, which forced us to change our usual automatic behaviours rapidly and effectively. Through extended exposure, automatic behaviours can become habits, which are complex behaviours tied to and triggered by certain events and performed without any specific goals or rewards (Ashby et al., 2010; Dickinson, 1985; Wood & Rünger, 2016). To rapidly adjust habits, the involvement of the executive control system is often required: we need to implement new actions consciously or avoid unwanted ones intentionally, like actively remembering ourselves to switch off the light when we leave a room or stopping ourselves from shaking hands upon meeting someone for hygiene reasons. Alternatively, habits may adjust without conscious effort when the changed environment forces them: for example, our roommate could unplug our unused charger every time, and maybe one day we realize that we have been similarly unplugging the charger for some time. Or, our co-worker has been greeting us with a fist bump every day since the beginning of the pandemic, and now we happen to do the same with our friends naturally.

From a cognitive point of view, to succeed in habit change, we need to simultaneously develop a new habit and unlearn—or at least fully inhibit—the old one (Hogarth et al., 2013; Szegedi-Hallgató et al., 2017). However, changing habits is challenging as the old behaviour seems to be hard to break (Poldrack, 2021). Research on habit change goes back a long way, yet its neurocognitive background is still poorly understood in the healthy human mind (Hardwick et al., 2019; Luque et al., 2020). Moreover, while the engagement of goal-directed behaviours is a common and seemingly obvious response, very little is known about how these interact with the procedural learning and memory processes underpinning habit change (Brevers et al., 2021; Quinn et al., 2010).

To conclude, although both the procedural memory system and the executive control system have received much scientific attention, many critical gaps and unanswered questions remain about their interplay during behaviour adaptation. In my doctoral research, I aimed to make steps towards addressing these shortcomings through five empirical studies.

II. Main questions of the dissertation

i. *Do errors contribute to the retrieval of an automatic behaviour in order to enhance task adaptation?* Performance monitoring, especially the processing of erroneous actions, is essential to maintain goal representations and achieve task goals. **Study 1** investigated how error processing takes place during the retrieval of an automatic behaviour to enhance adaptation. To answer this question, I investigated the event-related brain potential (ERP) correlates of error processing as well as the behavioural correlates of error-related task adaptation (post-error slowing, PES). The experimental design enabled us to test the interplay of procedural memory and the executive control system during acquisition and retrieval of an automatic behaviour without experimentally manipulating either of the two systems.

ii. *When and to what degree can we adjust automatic behaviours when the environment becomes unpredictable without any noticeable change at the surface level?* **Study 2** investigated the changes in automatic behaviours induced by changes in the environment's deep structure, without engaging the executive control system. First, I investigated the acquisition of a habit-like behaviour, then probed the updating of this behaviour following unsignalled structural changes introduced in the task.

iii. *Does procedural learning remain intact when attention is divided between concurrent tasks and task goals?* Next, I investigated whether we can successfully acquire automatic behaviours in a distracting environment where the engagement of the executive control system is experimentally manipulated. **Study 3** tested if and how the division of attention between concurrent tasks and task goals impact procedural learning. In addition, this study focused on another crucial aspect of the procedural memory system: the long(er)-term retention of the acquired behaviour and investigated whether divided attention during acquisition hinders the procedural memory.

iv. *How does response inhibition influence the rewiring of automatic behaviours?* **Study** 4 focused on the procedural memory vs. executive control system interplay during changing habit-like behaviours and probed whether we could ease the challenging process of habit change by inhibiting

the unwanted behaviour. More precisely, this study investigated the effect of response inhibition on the rewiring of automatic behaviours.

v. *How does procedural learning and interference suppression influence one another when simultaneously involved in fulfilling task goals?* In addition to the four main questions of the dissertation, the **Supplementary Study** (Appendix I.) targeted the relationship of procedural learning and the suppression of events interfering with the current task goals by manipulating the engagement of the latter process.

To sum up, Study 1 and Study 2 investigated behaviour adaptation without manipulating either the procedural memory system or the executive control system. Then, Study 3 and the Supplementary Study experimentally manipulated the engagement of the executive control system during the acquisition of automatic behaviours, with the former taking the question further to the retention of the acquired behaviour over an offline delay. Finally, Study 4 focused on changing these automatic behaviours in parallel with the engagement of the executive control system. In the following chapters, I will elaborate on the background of the procedural memory system and the executive control system, the theoretical accounts describing their relationship as well as the unclear issues and unanswered questions in the literature. Finally, I will provide a more detailed summary of the studies included in this dissertation.

III. Graphical summary of the dissertation

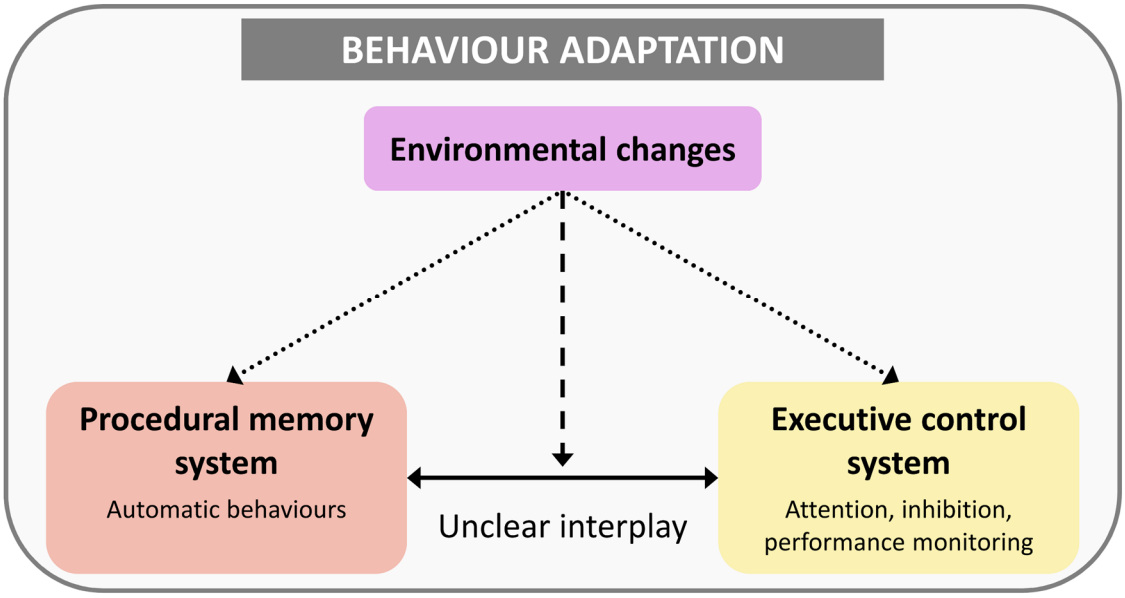

Figure 1. Schematic representation of processes contributing to behaviour adaptation. Successful behaviour adaptation relies on both automatic (illustrated by orange colour) and goal-directed behaviours (yellow). So far, the interplay between these two types of behaviours (solid line) is unclear: previous research suggests competitive/interfering, cooperative, or independent operation. Sometimes, however, environmental changes (purple) force us to adjust our automatic or goal-directed behaviours (dotted lines) and may influence their interplay as well (dashed line). The studies included in the dissertation aimed to target some of these interactions from different perspectives and methodological approaches.

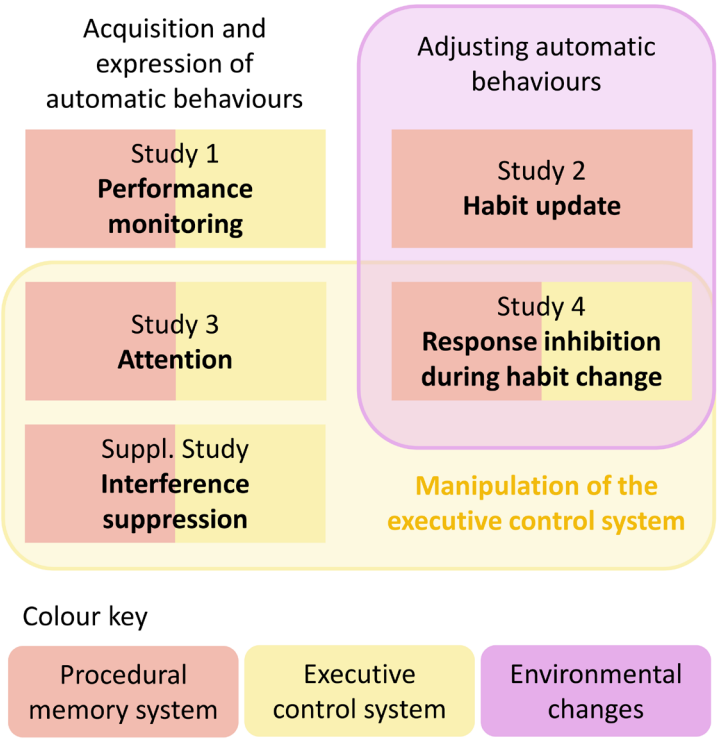

Figure 2. Overview of the studies included in the dissertation. In Study 1, we investigated the interplay of automatic and goal-directed behaviours during behaviour adaptation without any manipulations by focusing on the electrophysiological correlates of performance monitoring. In Study 3 and the Supplementary Study, we manipulated the engagement of the executive control system, namely attention and inhibition of interfering events and examined the acquisition of automatic behaviours in this way. Study 2 and Study 4 focused on behaviour adaptation when changes occur in the environment, illustrated by a purple background shading. In Study 2, we investigated the updating of automatic behaviours when the executive control system is not engaged, whereas, in Study 4, we manipulated the engagement of the executive control system, namely response inhibition, during behaviour change. From another perspective, Study 1 and Study 2 investigated behaviour adaptation without manipulating the engagement of the executive control system, while Study 3, Study 4 and the Supplementary Study directly manipulated the corresponding behaviours illustrated by a yellow background.

IV. Theoretical background

In this chapter, I will describe the two neurocognitive systems underpinning automatic and goal-directed behaviours contributing to behaviour adaptation. First, I will introduce the procedural learning and memory system with an emphasis on its contribution to behaviour change. I will also address some of the key methodological issues related to procedural memory. Second, I will cover the executive control system following a similar logic. Finally, I will briefly review the literature on the interaction between these two systems.

i. The procedural memory system

Procedural learning is a broad concept that covers the acquisition of complex automatic behaviours (Squire et al., 2004; Ullman, 2004). It is a fundamental ability contributing to numerous cognitive processes, such as language or perceptual categorization (Conway, 2020; Zwart et al., 2019), and it allows us to adjust our behaviour to the environment without effort (Hikosaka & Isoda, 2010). At the behavioural level, procedural learning and memory are characterized as implicit, incidental, (relatively) slowly encoded, and robust. It is implicit, that is, acquisition and expression take place without conscious access to the acquired behaviour or even the learning situation itself (Reber & Squire, 1994). It is incidental as intention and effort are not required for the acquisition or expression of the acquired behaviour (Perruchet & Pacton, 2006; Turk-Browne et al., 2005). Encoding of procedural memories usually takes place relatively slowly through repeated exposure as opposed to, for instance, episodic memories where a single exposure can result in a long-lasting memory trace (Henke, 2010). Finally, the acquired behaviour is robust, as per it is retained during the offline period following acquisition (Arciuli & Simpson, 2012; Gómez, 2017; Kim et al., 2009; Simor et al., 2019), it is resistant to long-term forgetting (Kóbor et al., 2017; Romano et al., 2010), interfering information (Szegedi-Hallgató et al., 2017), and cannot be flexibly altered (Henke, 2010). At the neural level, procedural learning is linked to large-scale brain networks consisting of cortico-basal ganglia-cerebellar circuits and the medial temporal lobe, with a supposed key role of the striatum (Batterink et al., 2019; Conway, 2020; Graybiel & Grafton, 2015; Janacsek et al., 2020; Squire et al., 2004).

Procedural learning underlies the formation of skills and habits. While these both require an extended period of exposure, they are fundamentally different. Skills are well-

learnt and resilient behaviours that can be executed with precision and little variety. Importantly, although a large proportion of skills is automatic, the execution itself is intentional and often consciously controlled (Du et al., 2022; Graybiel & Grafton, 2015). Therefore, skills are not addressed in this dissertation. Habits are traditionally defined as obligatory stimulus-response associations that are automatically triggered and elicited by an environmental stimulus or context and insensitive to changes in the outcome of the behaviour (Dickinson, 1985). Nevertheless, this definition comes from animal studies and thus cannot fully describe habits in humans (Foerde, 2018; Robbins & Costa, 2017). Alternatively, human habits can be defined as complex automatic behaviours that we are tied to, that are performed automatically and with little effort, and that can only be suppressed by conscious control (Du et al., 2022; Hardwick et al., 2019; Wood & Rünger, 2016). Habits are often associated with a negative connotation in our everyday life—think of the expressions "creature of habits" or "by force of habit". However, habits help us to switch into an "autopilot mode" in a familiar environment and save mental resources for additional tasks. When it comes to the necessity of changing habits, behaviour adaptation processes face a major challenge (Poldrack, 2021). So far, despite habit change being extensively studied in non-human animals and clinical populations, there have been only a few successful attempts to describe the basic cognitive processes involved in habit change (Krakauer & Shadmehr, 2006; Luque et al., 2020; Szegedi-Hallgató et al., 2017).

The procedural memory system is linked to another crucial aspect of smooth and effective behaviour adaptation: the ability to form predictions about future events based on recurring environmental patterns with probability-based relationships (Conway, 2020; Frost et al., 2019; Siegelman et al., 2017; Batterink et al., 2019; Conway, 2020)). By extracting these patterns, expectations about upcoming events can be made allowing for preparation to changes of the noisy environment (Bubic et al., 2010).

Experimental paradigms assessing procedural learning

Procedural learning is most often studied by (probabilistic) sequence learning tasks or probabilistic categorization tasks in different sensory modalities or cognitive domains (e.g., auditory tasks targeting [artificial] language learning, purely visual shapes, or visuomotor associations; Conway, 2020; Frost et al., 2019; Romberg & Saffran, 2010; Shohamy et al., 2008). It is still debated whether performance on these tasks models the same or distinct processes (Bogaerts et al., 2022; Frost et al., 2015); thus, in my doctoral dissertation, I focused only on learning in a visuomotor probabilistic sequence learning

task. Namely, I used various versions of the prominent Alternating Serial Reaction Time (ASRT) task (J. Howard & Howard, 1997; Kóbor et al., 2019; Nemeth, Janacsek, Londe, et al., 2010) which has good reliability, outperforming most sequence learning tasks (Farkas et al., 2022; Stark-Inbar et al., 2017).

The ASRT task is a four-choice reaction time (RT) task where, unbeknownst to participants, the stream of stimuli is defined by a repeating regularity. Participants are asked to press the button corresponding to the position/direction of the stimulus as fast and as accurately as possible. Within the repeating regularity, predefined stimuli alternate with randomly selected ones. One example of such regularity is the 1 – r – 3 – r – 2 – r – 4 – r sequence, where numbers denote the four predefined location on the screen or spatial direction of an arrow and 'r' denotes to a randomly chosen location/direction. Due to the alternating nature of the stimulus stream, some runs of consecutive trials (so-called triplets) are more probable than others. In the example above, 1 – r – 3 and 4 – r – 1 appear with a greater probability as these are presented in every repetition of the sequence (high-probability triplets). These triplets can also appear by chance consisting of two random trials and one pattern trial as the middle element. On the other hand, 1 – P – 2 and 4 – P – 3 (where 'P' denotes one of the predefined elements of the regularity) appear with a lower probability as these can be formed by chance only (low-probability triplets). For all triplets, the third element (*n*) of a triplet is predictable by the first one (*n*-2) with a given probability, while the middle element (*n*-1) does not have a predictive value. High-probability triplets constitute 62.5% of all trials, while the remaining 37.5% are constituted by low-probability triplets. Through practice, performance on the high-probability triplets improves, whereas it falls or stagnates on the low-probability ones. The magnitude of procedural learning can be measured as the difference in performance between these two triplet types.

Over the years, many different versions of the ASRT task have been used and published. A notable version is the so-called cued ASRT task, where the repeating predefined trials are indicated (cued) by visually different stimuli than the random ones (Kóbor et al., 2018; Nemeth, Janacsek, & Fiser, 2013; Tóth-Fáber et al., 2021). Additionally, participants are informed about the presence of a repeating sequence in the task but not the underlying probability structure. This allows us to simultaneously measure different aspects of learning (i.e., acquiring the cued sequence order vs. the hidden probability-based structure). Another relevant version of the ASRT task is

characterized by a more complex regularity design: it contains an interfering regularity. In this task version, the underlying regularity is changed at some point in the task, which enables us to challenge the acquired behaviour (Kóbor et al., 2017; Zavecz et al., 2020). When practice is extended on the interference regularity, behaviour (habit) change can be induced in the task (Szegedi-Hallgató et al., 2017). In my dissertation, I applied the original, the cued, and two different interference versions of the ASRT task as well as created new task versions by combining the task with additional paradigms of goal-directed behaviours.

Aspects of learning in the procedural memory system

The ASRT task is a powerful tool as it allows for assessing several aspects of the procedural memory system. In earlier publications, it was commonly linked to skill learning (e.g., Hallgató et al., 2013; Janacsek et al., 2012; Nemeth & Janacsek, 2010). Importantly, more recent publications suggest that skills are flexible and expressed intentionally (Du et al., 2022), unlike the rigid and implicit behaviour acquired in this task. In contrast to skills, habits and habit-like behaviours have similar characteristics to the behaviour learnt in the ASRT task (Ashby et al., 2010; Du et al., 2022; Graybiel & Grafton, 2015), yet this term has not been frequently used so far (Horváth et al., 2022). Sequence learning is another commonly used term, originating from the literature on deterministic Serial Reaction Time (SRT) tasks (e.g., Fletcher et al., 2005; Song et al., 2007; Stark-Inbar et al., 2017). This term can be somewhat misleading when used for the ASRT task specifically, as the most commonly used measure of this task relates to the extraction and acquisition of the probability-based structure instead of the repeating sequence order (Kóbor et al., 2019; Szegedi-Hallgató et al., 2019). Meanwhile, acquiring the repeating sequence is indeed possible in the task, but, in the original (non-cued, fully implicit) version, it seems to require extended practice (at least nine sessions, more than 15.000 trials; D. Howard et al., 2004), and relatively little is known about how exactly this process takes place (Kóbor et al., 2019; Szegedi-Hallgató et al., 2019). Sequence learning can be effectively induced in the cued version of task (Kóbor et al., 2018; Simor et al., 2019). This version enables the engagement of more intentional and conscious learning processes that can be contrasted with the incidental acquisition of automatic behaviours within the task. Finally, the term statistical learning is another often-used term to describe learning in the ASRT task (Arciuli, 2017; Obeid et al., 2016; Szegedi-Hallgató et al., 2019), which refers to the efficient extraction and acquisition of probability-based

regularities in the environment and originates from the research line of language learning in infancy (Saffran et al., 1996). Overall, with the appropriate modification, the ASRT can measure at least three different aspects of the procedural memory system: habit learning, sequence learning, and statistical learning.

Some of these terms put the emphasis on the way of extraction and the nature of the acquired knowledge (statistical or sequence learning), whereas others highlight the type of behaviour developed by practicing the task (skill, habit, or procedural learning). While both approaches have their benefit, using various terms to label the same aspect of learning in the ASRT task can easily lead to conceptual discrepancies in the literature and separation of related research lines. In the studies included in this doctoral dissertation, we also used various terms to best describe learning in the specific task version applied in the given study. In Study 1, where we applied the cued version of the task, we focused on the quick learning of the (cued) sequence order which then could have possibly been retrieved to achieve better task performance. To grasp the essence of these processes, we used the term "probabilistic sequence retrieval". In Study 2 and 3, we focused on the acquisition of the probability-based structure present in the task under implicit and incidental conditions. Accordingly, we used the terms "statistical learning" and "implicit acquisition of second-order transitional probabilities", with the latter being closely related but not fully corresponding to the former. In Study 4, we labelled learning as "habit learning" since practice here was extended and thus the formation of habit-like behaviours was enabled in the task. Finally, in the Supplementary Study, we opted for the umbrella term of procedural learning to connect to a wider scope in the literature. Taking into consideration the different aspects of learning the ASRT task can grasp, I use the terms 'procedural learning' and 'procedural memory' in my dissertation as it can encompasses all of those targeted in the five studies.

To summarize this subchapter, procedural learning and memory are undoubtedly important for successful behaviour adaptation; nevertheless, it is rarely discussed from such a point of view leaving a gap in the literature. In this dissertation, I aim to cover the various aspects of the procedural memory system from the initial acquisition of automatic behaviours through their expression to the formation and change of habits.

ii. The executive control system

Successful goal-directed behaviours rely on an executive control system. This system contains numerous cognitive processes that act together in an orchestrated way to achieve internal and external goals (Friedman & Robbins, 2022). Goal-directed behaviours have been extensively studied from various scientific directions. Therefore, it is unsurprising that there are several different terms and definitions to describe these processes, such as executive functions (Miyake et al., 2000), cognitive control (Botvinick et al., 2001; Miller, 2000), or executive control (Pessoa, 2009). The executive control system depends on large-scale neural networks of the prefrontal cortex (PFC) and other cortical (among others, the posterior parietal regions and the anterior cingulate cortex) and subcortical (including the thalamus and the basal ganglia) brain regions. Though these networks are characterized as distinct functional and anatomical units, they act together and not in isolation to successfully execute goal-directed behaviours (Arnsten & Rubia, 2012; Friedman & Robbins, 2022; Menon & D'Esposito, 2022). In this dissertation, I follow the comprehensive theoretical account proposed by Bari & Robbins (2013) and conceptualize the executive control system accordingly.

In their concept, Bari & Robbins (2013) identified two core components and four auxiliary components of goal-directed behaviours that need to function interactively for successful behaviour adjustment. One of their core components is attention. Attention is responsible for selecting which stimuli are to be attended to as well as for processing the relevant changes in the environment. The second, and probably the most significant, core component is inhibition or inhibitory control. Inhibition is a compound process with various aspects. In general, it can be described as the cognitive function for suppressing prepotent but unwanted actions, filtering interfering and distracting information, and stopping irrelevant cognitive and emotional processes. Attention and inhibition are continuously supported by performance monitoring processes whose task is to detect and signal any suboptimal actions or drops in performance. In case of such slips, the processes of updating, selection, and shifting are activated in order to update task goals, select a new plan, and shift resources accordingly (Bari & Robbins, 2013).

It is important to note, however, that despite this concept being relatively comprehensive, the executive control system is yet to be fully understood. A crucial issue is the unity and diversity of these processes (Duncan et al., 2010; Friedman & Robbins, 2022; Miyake et al., 2000). There is behavioural, neural, and clinical evidence for both

an overlap (unity, i.e., correlated processes) and a differentiation (diversity, i.e., uncorrelated processes) between the processes involved in the executive control system. The full description of the phenomenon goes beyond the scope of this dissertation. Still, according to Friedman & Robbins (2022), inhibition is most probably responsible for unity as it explains the covariance observed between tasks assessing the executive control system and its neural background. The remaining processes (e.g., shifting, updating) are thought to be contributing to diversity, that is, to the observed variance in these specific tasks. To put it simply, all sorts of executive control processes seem to require some level of inhibition. In my doctoral research, I focused on the two core components, attention and inhibition, as well as on performance monitoring as an important auxiliary component (based on Bari & Robbins, 2013). I chose these processes because they are possibly involved in any goal-directed behaviours (attention and inhibition due to their central role and performance monitoring due to the constant need for monitoring the outcome of the behaviour).

Components of the executive control system and their corresponding experimental paradigms

Attention – Attention can refer to a wide range of processes from a minimal level necessary for stimulus processing to sustained focus and the filtering of relevant information in a noisy environment (Hommel et al., 2019). Earlier research distinguished between an intensity and a selectivity aspect of attention: the former referring to arousal and sustained attention related processes and the latter referring to processes enabling to attend to a certain set of information only, such as focused and divided attention (van Zomeren & Brouwer, 1994). More recent studies define the aspects of attention based on large-scale neural networks. Among others, the dorsal and ventral attention networks have been linked to involuntary and voluntary redirection of attention, respectively, and the salience network has been linked to attention towards the most relevant external or internal information (Bressler & Menon, 2010; Menon & D'Esposito, 2022; Vossel et al., 2014). Alternatively, Posner and colleagues have identified three independent attentional networks: the alerting, the orienting, and the executive systems, the latter one showing overlap with other components of the executive control system, such as error detection and conflict resolution (Fan et al., 2002; Posner et al., 2016). From the viewpoint of goal-directed behaviours, attention is essential for selecting the relevant environmental events

and maintaining focus on these as well as on our goals (Lavie et al., 2004; Miller, 2000; Yeung, 2014).

The engagement of attention can be experimentally investigated by selective attention and divided attention paradigms. Selective attention refers to the filtering of which stimuli are to be attended to or ignored. In contrast, divided attention refers to the simultaneous execution of at least two concurrent tasks within the same stimulus stream (Jiménez & Mendez, 1999). It is challenging to determine which of the above-introduced networks support divided attention. So far, this process has been linked to the executive system of attention (Fernandez-Duque & Posner, 2001) and there is accumulating evidence to suggest that the PFC plays a key role in it (Johnson & Zatorre, 2006; Nebel et al., 2005; Salo et al., 2017; Vohn et al., 2007).

It is still unclear how an increased attentional load interacts with the procedural memory system (Jiménez & Mendez, 1999; Vékony, Török, et al., 2020). Thus, in Study 2, I introduced the manipulation of divided attention in the ASRT task. To do so, the cued version of the task was manipulated. In the cued task, participants ultimately had two goals: to discover and memorize the order of the cued repeating pattern trials and to meanwhile maintain sufficiently fast and accurate responses on all trials. However, instead of the usually applied self-paced task timing, stimuli were presented with a fast and fixed-paced time setting which made it difficult for participants to intentionally learn the repeating sequence (task 1) while maintaining a good response speed and accuracy (task 2). That is, their attention had to be divided between the two concurrent tasks. This was contrasted in a between-subject manner to a similarly fast and fixed-paced version of the fully implicit ASRT task, where participants' only task was to maintain good task performance.

Inhibition – Inhibition or inhibitory control is another broad term that has been used to describe various processes and phenomena since its emergence in the scientific literature (Bari & Robbins, 2013; Friedman & Robbins, 2022; Munakata et al., 2011). Based on the seminal partitioning of Nigg (2000), automatic, motivational, and effortful inhibition can be distinguished. From another perspective, aspects of inhibition can be defined based on different dimensions: behavioural (i.e., stopping the execution of unwanted actions or not letting interfering information exert their distracting effect) vs. cognitive (i.e., stopping irrelevant information to be maintained in the working memory; Harnishfeger, 1995; Kipp, 2005) or selective (cancelling a certain action while keeping

others active) vs. nonselective (i.e., stopping all actions; de Jong et al., 1995; van Boxtel et al., 2001). In a more recent attempt, Bari and Robins (2013) proposed that inhibition of manifest behaviour can be partitioned into response inhibition, deferred gratification, and reversal learning. To conclude, there have been several somewhat different but overlapping attempts to describe the many aspects of inhibition, but the full picture is still unclear.

There seems to be a consensus, however, that processes related to behavioural inhibition encompass two fundamental abilities: response inhibition (Luk et al., 2010; Menon et al., 2001; Ridderinkhof et al., 2004; Verbruggen & Logan, 2008b) and interference suppression (Luk et al., 2010; Miller & Cohen, 2003; Verbruggen et al., 2004), which can be separated at the neurocognitive level (Bryce et al., 2011; Brydges et al., 2012). It is important to note that evidence of various nature points towards that response inhibition and interference suppression are closely related and not necessarily separable at the behavioural level (Friedman & Miyake, 2004). Together, they contribute to effectively maintaining task goals and goal-directed information, making inhibitory control the core (and presumably exclusive) component of the executive control system (Aron, 2007; Aron et al., 2003; Friedman & Robbins, 2022; Miyake & Friedman, 2012).

The experimental manipulation of response inhibition or interference suppression is a promising candidate for studying the interplay between automatic and goal-directed behaviours. Response inhibition can be induced by introducing task events where responses are prohibited, such as in the Go/No-go task (Gordon & Caramazza, 1982) or the Stop-Signal task (Logan & Cowan, 1984). Interference suppression can be induced by presenting distracting events together with the target event, like in the Eriksen flanker task (Eriksen & Eriksen, 1974) or the Stroop task (Stroop, 1935). In my doctoral research, I investigated the interplay between inhibitory control and procedural learning in two ways. In the Supplementary Study, I introduced an interference suppression manipulation during procedural memory acquisition assessed via the ASRT task. Subsequently, I studied this interplay during habit change as well; that is, I introduced a response inhibition manipulation to the ASRT task during the rewiring of habit-like behaviours in Study 4. This manipulation modelled the common everyday attempt for stopping undesired habits.

Performance monitoring – For successful behaviour adaptation, we need to continuously monitor our behaviour and adjust it if we erred. Such processes can be

described as performance monitoring, with error processing as a core component (Gehring et al., 1993; Ullsperger & von Cramon, 2001), and can be closely examined via the method of ERPs (i.e., stereotypical electrophysiological responses of the brain to external or internal events; Coles et al., 1990). The different stages of error processing can be tracked by the error negativity (Ne or ERN; Falkenstein et al., 1991; Gehring et al., 1993) and the error positivity (Pe; Falkenstein et al., 1991; Overbeek et al., 2005). The Ne reflects the automatic detection that an error has occurred. In other words, this component can provide evidence if and how the executive control system detected that the provided response was not optimal, even in the absence of awareness to the erroneous action. The magnitude of the Ne is associated with, among others, the motivational significance and relevance of the error (Falkenstein et al., 1991; Hajcak et al., 2005), the discrepancy between the intended and the executed response (Falkenstein et al., 1991; Gehring et al., 2012), and the amount of conflict between the correct and incorrect response representations (Botvinick et al., 2001; Yeung et al., 2004). That is, a larger Ne suggests a larger error. The Pe, on the other hand, reflects the conscious evaluation of the error; that is, this component can indicate that a conscious representation of the committed error was formed. The magnitude of the Pe is associated with the amount of awareness that the response was incorrect (Endrass et al., 2007; Nieuwenhuis et al., 2001), the salience of the error (Ridderinkhof et al., 2009), and the level of confidence that an error was committed (Boldt & Yeung, 2015).

So far, it is unclear how automatic error detection and conscious error evaluation take place during and contribute to procedural learning and memory expression (Beaulieu et al., 2014; Ferdinand et al., 2010; Rüsseler et al., 2018). At the behavioural level, detection of errors and the subsequent behaviour adjustment processes can be tracked by, among others, the post-error slowing (PES) effect which refers to the phenomenon that RTs increase on the trial directly following an incorrect response (Danielmeier & Ullsperger, 2011; Ullsperger & Danielmeier, 2016). In Study 1, I focused on the Ne and Pe ERP components and the PES effect to investigate performance monitoring during the initial acquisition and subsequent retrieval of an automatic behaviour. These effects were contrasted to an embedded baseline process where adaptation to the task took place in the absence (or direct involvement) of procedural learning processes.

iii. The relationship between procedural memory and the executive control system

Previous studies led to controversial conclusions on the relationship between procedural learning and the executive control system. These can be roughly divided into two distinct approaches: the associative learning account (Deroost et al., 2012; Egner, 2014; Jiménez, Abrahamse, et al., 2020) and the competitive systems framework (Janacsek et al., 2015; Poldrack & Packard, 2003; Smalle et al., 2022).

On the one hand, the associative learning account originates from the observations that the resolution of and the adaptation to conflicting events, like in interference suppression or response inhibition tasks, can be supported by learning processes (Egner, 2007, 2014). Based on these observations, numerous studies have investigated the relationship between procedural learning and inhibition/inhibitory control in combined paradigms featuring both processes. The results are inconclusive, however. Some argue that procedural learning can support inhibition (Deroost et al., 2012; Koch, 2007), as procedural learning can lead to a less demanding conflict resolution by facilitating the binding of task-relevant information. Another line of research revealed an opposite direction: higher level of conflict in the task can lead to better procedural learning or the expression of procedural memory because of increased task demands promoting the reliance on learning processes (Coomans et al., 2011; Deroost et al., 2012; Deroost & Coomans, 2018; Deroost & Soetens, 2006). Finally, some studies found that inhibition and procedural learning are independent (Jiménez, Abrahamse, et al., 2020; Jiménez, Méndez, et al., 2020). There are some important critiques towards these studies, however: i) the applied deterministic sequence learning tasks are limited to a single aspect of the procedural memory system, ii) the simple deterministic regularity can easily become available to conscious processes, and iii) the tasks cannot closely model the complexity of automatic behaviours used in our everyday life.

The competitive systems framework, on the other hand, originates from the notion that the procedural memory system and the executive control system, when activated in parallel, compete for the same mental resources (Poldrack et al., 2001; Poldrack & Packard, 2003). Studies following this framework tested clinical populations (correlational designs) or applied interventional designs to manipulate the engagement of the executive control system and/or the PFC. So far, evidence for better/intact procedural learning when the PFC is less active/impacted has been found in alcoholic patients (Virag

et al., 2015), in autism (Nemeth, Janacsek, Balogh, et al., 2010), in non-invasive brain stimulation of the dorsolateral PFC (Ambrus et al., 2020; Smalle et al., 2022), in hypnosis (Nemeth, Janacsek, Polner, et al., 2013), in cognitive fatigue (Borragán et al., 2016), and in a dual-task situation (Foerde et al., 2006). Analogue to these studies, the simultaneous involvement of procedural memory and executive control processes in combined paradigms can lead to impaired acquisition and expression of automatic behaviours (Prutean et al., 2022; Vaquero et al., 2020). On the contrary, other pieces of evidence showed that the reduction in executive resources hindered subsequent procedural learning and memory expression (Thompson et al., 2014). Overall, the studies described above mostly investigated the interplay of procedural learning and the executive control system by i) manipulating the latter and ii) reducing/taxing it leading to one-sided and inconclusive results. Therefore, though mainly focused on complex, automatic, and incidental/implicit behaviours, these cannot fill in the gap left by the associative learning account.

To conclude this subsection, there are two distinguishable approaches to studying the interplay of automatic and goal-directed behaviour adaptation: the associative learning account using combined paradigms and the competitive systems framework using correlational and interventional designs. However, neither could answer the question of how this interplay takes place when complex automatic behaviours are acquired and expressed while goal-directed behaviours are involved in the task *simultaneously*. With Study 3, Study 4, and the Supplementary Study, I aimed to fill in this gap.

iv. Chapter overview

I believe that by understanding the different behaviours underpinning behaviour adaptation and their interaction, we can contribute to addressing recent challenges in our lives. We live in a world that changes faster than ever before, where we are surrounded by an increasing amount and variety of stimuli, and where we are urged to adjust our well-established habits as quickly as possible. Although both procedural learning and the executive control system have attracted considerable scientific interest so far, much remains to be discovered, especially about how exactly they influence one another. This dissertation aims to unravel some of the questionable points in the literature. To this end,

I have set out to systematically probe the interplay between these two systems with different aspects (statistical, sequence, and habit learning) and phases of learning (acquisition, retention, and habit adjustment/change) and with different components of the executive control system (error processing, divided attention, response inhibition, and interference suppression). In the next sections, I will present altogether five studies focusing on various combinations of these processes, with a follow-up analysis of individual differences providing additional insight into the nature of the procedural memory vs. executive control systems interplay.

V. Study 1: Do errors contribute to the retrieval of an automatic behaviour in order to enhance task adaptation?

Publication:

Horváth, K., Kardos, Z., Takács, Á., Csépe, V., Nemeth, D., Janacsek, K., & Kóbor, A. (2021). Error processing during the online retrieval of probabilistic sequence knowledge. *Journal of Psychophysiology, 35*(2), 61-75.

Article

Error Processing During the Online Retrieval of Probabilistic Sequence Knowledge

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Abstract: Adaptive behavior involves rapid error processing and action evaluation. However, it has not been clarified how errors contribute to automatic behaviors that can be retrieved to successfully adapt to our complex environment. Automatic behaviors strongly rely on the process of probabilistic sequence learning and memory. Therefore, the present study investigated error processing during the online retrieval of probabilistic sequence knowledge. Twenty-four healthy young adults acquired and continuously retrieved a repeating stimulus sequence reflected by reaction time (RT) changes on a rapid forced-choice RT task. Performance was compared with a baseline that denoted the processing of random stimuli embedded in the probabilistic sequence. At the neurophysiological level, event-related brain potentials synchronized to responses were measured. Error processing was tracked by the error negativity (Ne) and the error positivity (Pe). The mean amplitude of the Ne gradually decreased as the task progressed, similarly for the sequence retrieval and the embedded baseline process. The mean amplitude of the Pe increased over time, likewise, irrespective of the type of the stimuli. Accordingly, we propose that automatic error detection (Ne) and conscious error evaluation (Pe) are not sensitive to sequence learning and retrieval. Overall, the present study provides insight into how error processing takes place for the retrieval of sequence knowledge in a probabilistic environment.

Keywords: adaptation, error negativity, error positivity, error processing, probabilistic sequence learning

Adaptive behavior requires a monitoring system that evaluates actions, adjusts performance to the environmental conditions, and detects the possible negative outcomes, such as errors. Although errors have been widely researched in the context of learning in general (Gehring, Goss, Coles, Meyer, & Donchin, 2018; Rüsseler, Münte, & Wiswede, 2018), it has remained less clear how error processing takes place during the retrieval of the acquired knowledge. Probabilistic sequence learning enables us to form automatic behaviors that can be retrieved to successfully adapt to the environment (Armstrong, Frost, & Christiansen, 2017; Turk-Browne, Scholl, Johnson, & Chun, 2010). The most prominent neurophysiological correlates of error processing are the error negativity (Ne; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) or error-related negativity (ERN; Gehring, Goss, Coles, Meyer, & Donchin, 1993) and the error positivity (Pe; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) event-related brain potential (ERP) components. Here we use these neurophysiological markers to investigate the different aspects of error processing in an intentional probabilistic sequence learning task. We report evidence that both the Ne and the Pe are sensitive to performance improvement and adaptation to the task, but these components are not affected by the predictability of the sequence.

The Ne is a response-locked negativity of fronto-central maximum peaking approximately 50–150 ms after an error is committed by the individual (Falkenstein et al., 1991; Gehring et al., 1993). The Ne has been shown to indicate the automatic detection of an erroneous response

(i.e., independently of the error-apperception; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). The Ne is usually followed by the Pe that is a response-locked positivity occurring with a centro-parietal maximum in a wider time window, ca. 100–500 ms after the onset of the erroneous response (Falkenstein et al., 1991; Overbeek, Nieuwenhuis, & Ridderinkhof, 2005). The Pe has been predominantly linked to conscious error evaluation (Nieuwenhuis et al., 2001).

The exact underlying processes of the Ne are still debated; nevertheless, several theories have emerged so far. According to the *error detection/mismatch theory*, the magnitude of the Ne reflects the discrepancy between the actual and the intended response (Bernstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991; Gehring et al., 1993). The *reinforcement learning theory* (Holroyd & Coles, 2002) claims that the Ne serves as a reinforcement learning signal when the outcome of the behavior is worse than expected. The *conflict theory* (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter et al., 1998; Yeung, Botvinick, & Cohen, 2004) postulates that the Ne is a result of a process that continuously evaluates coactive and competing response representations. Finally, the *motivational significance theory* states that the magnitude of the Ne reflects the emotional significance of an error (Gehring et al., 1993; Hajcak, Moser, Yeung, & Simons, 2005): The larger the significance of the error, the larger the Ne.

The functional significance of the Pe is still argued, as well. This component is most often linked to error awareness (Endrass, Reuter, & Kathmann, 2007; Nieuwenhuis et al., 2001). In turn, another approach claims that the Pe is a P3b-like component reflecting error relevance (Falkenstein et al., 1991; Overbeek et al., 2005; Ridderinkhof, Ramautar, & Wijnen, 2009). A more recent line of research states that the Pe reflects the accumulated decision evidence that an error has occurred (Boldt & Yeung, 2015; Steinhauser & Yeung, 2012).

Previous studies investigating error processing during sequence knowledge formation mostly focused on the initial acquisition processes (Beaulieu, Bourassa, Brisson, Jolicoeur, & De Beaumont, 2014; Ferdinand, Mecklinger, & Kray, 2008; Rüsseler, Kuhlicke, & Münte, 2003; Rüsseler et al., 2018) and usually investigated only the Ne (but see Ferdinand et al., 2008). Further, the retrieval of sequence knowledge has been approached by the investigation of stimulus- or correct response-related ERP components so far (Ferdinand, Rünger, Frensch, & Mecklinger, 2010; Miyawaki, Sato, Yasuda, Kumano, & Kuboki, 2005; Rüsseler & Rösler, 2000; Steinemann, Moisello, Ghilardi, & Kelly, 2016). Thus, the question remains how error processing takes place during the retrieval of the acquired sequence knowledge.

To fulfill this gap, we introduce a probabilistic sequence learning task that involves the fast initial acquisition of a repeating sequence followed by the continuous *retrieval of this sequence* (Kóbor et al., 2018; Nemeth, Janacsek, & Fiser, 2013; Simor et al., 2019; Song, Howard, & Howard, 2007a, 2007b). Namely, participants perform a rapid forced-choice RT task, in which stimulus presentation follows a repeating probabilistic sequence that can be learned and retrieved during task solving to achieve a better performance. The probabilistic nature of the sequence enables us to measure a retrieval-free baseline process, as well, that refers to the incidental RT improvement on the embedded random elements in parallel with the retrieval of the repeating sequence. Participants are asked to react to the direction of the stimuli according to a simple stimulus – response mapping rule. Over the course of continuous task performance, we investigate the possible change of the Ne and the Pe components synchronized to the onset of the responses.

Although theories approach the Ne from different aspects, a converging conclusion can be drawn: For the acquired sequence knowledge, all theories predict an increasing Ne over the task, since it is presumable that any hypothesized underlying process of the Ne would be facilitated by learning and retrieval processes. In contrast, the Ne for the embedded baseline is predicted to remain similar throughout the task. Accordingly, we expect an increase in the amplitude of the Ne selectively for the repeating sequence, as the retrieved knowledge strengthens. Similarly, it is presumable that learning and retrieval processes can facilitate the processes underlying the Pe, therefore, the above-detailed approaches predict an increasing Pe for the repeating sequence and an unvarying Pe for the embedded baseline. Thus, we also expect an increasing Pe for the repeating sequence opposing random events in the task, as the acquired representations become more consciously available.

Methods

Participants

Data were collected in the study reported by Kóbor et al. (2018), where stimulus-locked ERPs were analyzed for correctly responded trials. Forty-one healthy young adults participated in the experiment. One of them was excluded because of technical reasons. For the purpose of the present study, the inclusion criterion was set to a minimum of eight erroneously responded, artifact-free EEG segments for both the sequence and random trial types (see details below) in each time period of the task (Meyer, Riesel, & Proudfit, 2013; Olvet & Hajcak, 2009). Therefore, further 16 participants were left out from the original sample due to the low number of erroneous responses or excessive

artifacts. Hence, 24 participants (age range: 19–24 years, M = 20.9 years, SD = 1.4 years; $M_{education}$: M = 14.4 years, SD = 1.4 years; male/female ratio: 9:15) remained in this final sub-sample.

Handedness was measured by the Edinburgh Handedness Inventory (Oldfield, 1971); the laterality quotient varied between 0 and 100 (M = 71.09, SD = 21.27), where −100 means complete left-handedness and 100 means complete right-handedness. Participants had normal or corrected-to-normal vision, none of them reported histories of any psychiatric and/or neurologic conditions, and none of them were taking any psychoactive medications. All participants provided written informed consent before enrolment and received payment (ca. 10 €) or course credit for taking part in the experiment. The study was approved by the United Ethical Review Committee for Research in Psychology (EPKEB) in Hungary and was conducted in accordance with the Declaration of Helsinki.

Task and Procedure

Probabilistic sequence knowledge formation was measured by a modified cued version of the Alternating Serial Reaction Time (ASRT) task (Kóbor et al., 2018; Nemeth, Janacsek, & Fiser, 2013). In this task, an arrow stimulus appears at the center of the screen. Participants are instructed to press the response key corresponding to the spatial direction of the arrow (left, up, down, or right) on a response box (Cedrus RB-530, Cedrus Corporation, San Pedro, CA) as fast and as accurately as possible using their left or right index finger or thumb, respectively.

The presentation of the arrow stimuli follows an eight-digit sequence within which predefined pattern and random (r) trials alternate. One example of the sequence is 1–r–2–r–4–r–3–r, where numbers represent the four possible spatial directions (1 = left, 2 = up, 3 = down, 4 = right) and "r"s denote randomly chosen spatial directions out of them. The sequence structure is cued by different colors: Predefined pattern trials appear as black arrows, while random trials appear as red ones (Figure 1A). Participants are informed that the presentation of black arrows follows a predefined sequence, while red arrows point to randomly chosen spatial directions. They are instructed to learn the exact order of the black arrows.

In the present study, we examine error processing during probabilistic sequence retrieval, hence, we focus on the differences between pattern trials and the embedded random trials. However, due to the alternating nature of the sequence, a hidden predictability structure emerges in the task based on the *frequency of chunks of trials* – referred to as triplets – instead of single trials. Some of these triplets occur more frequently than others. Each trial is categorized as either the third element of a high- or a low-frequency triplet; therefore, the terms "trial" and "triplet" are used interchangeably for the remainder of the paper. Frequency also defines the predictability of a triplet's third element. This structure results in two different types of random trials, which are differently related to learning and retrieval processes. While the pattern trials always appear with high frequency, random trials appear either with high- or low-frequency. Therefore, while frequent random trials become as predictable as the pattern ones, infrequent random trials remain less predictable. Overall, the combination of the sequential and the frequency properties results in three possible trial types: pattern trials, high-frequency random trials, and infrequent random trials (Figure 1B; for more details, see Kóbor et al., 2018; Nemeth et al., 2013; Simor et al., 2019). In the present study, all high-frequency random trials were excluded from the analyses to avoid possible retrieval-related confounds. Previous ASRT studies showed that the acquisition of sequence knowledge takes place early in the cued version of the task (Kóbor et al., 2018; Nemeth et al., 2013; Simor et al., 2019). It is, therefore, presumable that further RT improvement is based on the *online retrieval* of this knowledge. Generally, RTs to the infrequent random trials also improve along with decreasing accuracy, which is not explained by speed-accuracy trade-off (Tóth et al., 2017). From now on, random trials are referred to as *infrequent random* trials.

Thirty blocks of the ASRT task added up the experiment and the whole procedure lasted about 2.5 hr including the application of the electrode cap. One block contained 85 trials: The eight-digit alternating sequence repeated 10 times in each block after 5 warm-up trials consisting only of random trials. To ascertain that conscious sequence knowledge emerges, a *sequence report* was administered after each block. Participants were asked to type the order of pattern trials using the same response keys as in the ASRT task. This method allowed us to determine the duration (in terms of the number of blocks) participants needed to learn the sequence correctly as defined by consistently reporting the same sequence from that point on in the remaining blocks.

The structure of the task was the following. An experimental trial started with the presentation of the stimulus (arrow) for 200 ms. Then, a blank screen occurred until the participant gave a behavioral response but no longer than 500 ms. After the response, a blank screen was presented for a fixed delay of 700 ms before the next trial started. This is called as response-to-stimulus interval (RSI). Participants could also provide a response during the 200-ms time window of stimulus presentation; in that case, the stimulus disappeared after the response onset, followed immediately by the RSI. A blank screen was presented for 500 ms after every erroneous response, followed by a black "X" at the center of the screen for another

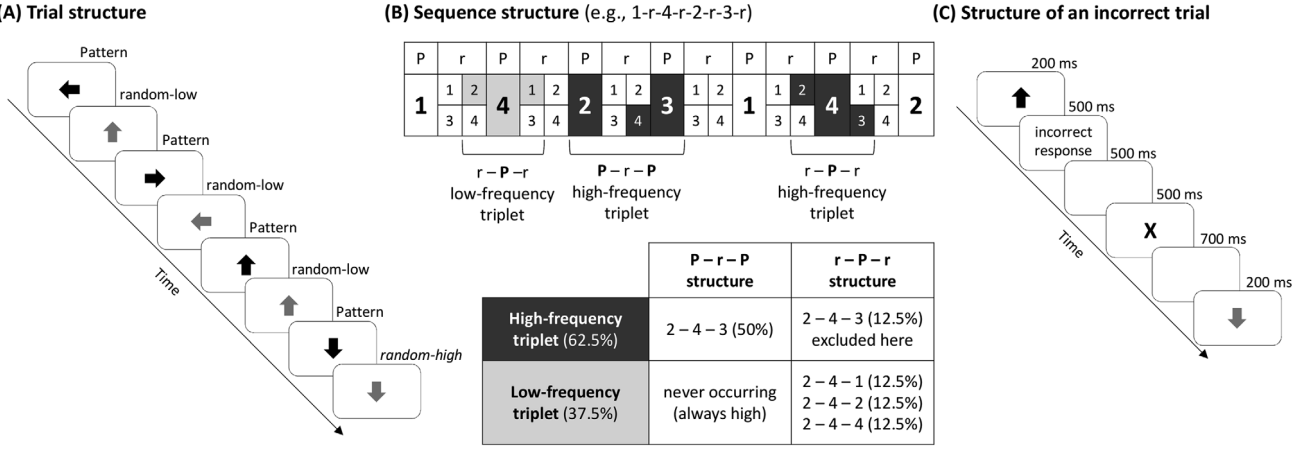

Figure 1. Schematic of the task. (A) In the cued Alternating Serial Reaction Time (ASRT) task, the presentation of the stimuli follows an eight-digit alternating sequence, within which predefined pattern (P) trials alternate with random (r) ones. Pattern trials are marked by black and random trials are marked by red (shown by gray on this figure). (B) In the sequence structure, numbers denote the four spatial directions (1 = left, 2 = up, 3 = down, 4 = right) of the arrows. High-frequency triplets are denoted with dark gray shading and low-frequency triplets are denoted with light gray shading. We determined for each pattern and random stimulus whether it was the last trial of a high- or a low-frequency triplet, thus, three different trials could occur: pattern (P–r–P structure, always high-frequency), random-high (high-frequency with r–P–r structure) and random-low (low-frequency with r–P–r structure). (C) Timing and strucutre of an erroneous trial.

500 ms (Figure 1C). For the lack of response, a black "!" was displayed for 500 ms. These warning stimuli served as visual feedback for error commission or missing response, respectively. RSIs were presented after both warning stimuli. If the participant provided a further response to correct the erroneous or missed trial, it influenced neither the presentation nor the timing of the next trial; thus, the task proceeded without providing the correct response. After each block, the participant received feedback about the mean reaction time and accuracy on the predefined pattern trials (black arrows) in the given block. The ASRT task was written in and run by the Presentation software (v. 18.1, Neurobehavioral Systems, Inc., Berkeley, CA, USA), and stimuli were presented on a 19″ CTR screen with a viewing distance of 125 cm.

EEG Recording and Analysis

The EEG measurement was conducted in an acoustically attenuated, electrically shielded, dimly lit room. The EEG was recorded with 64 Ag/AgCl electrodes, placed according to the international 10-20 system, using Synamps amplifiers and Neuroscan software 4.5. (Compumedics Neuroscan, Charlotte, NC, USA). The tip of the nose served as reference and the electrode AFz served as ground. Vertical and horizontal eye-movements were measured by electrodes attached above and below the left eye, and in the left and right outer canthi. The sampling rate was 1000 Hz, electrode impedance levels were kept below 10 kΩ, and a 70-Hz low-pass filter (24 dB/oct) was applied online.

Data analysis was conducted in the Brain Vision Analyzer software (Brain Products GmbH, Gilching, Germany). First, a 0.5 to 30-Hz band-pass filter (48 dB/oct) and a 50-Hz notch filter were applied offline. Then, independent component analysis (ICA) was used to correct vertical and horizontal eye-movements and heartbeats (Delorme, Sejnowski, & Makeig, 2007). After, the EEG data were re-referenced to the average activity of all electrodes. The continuous EEG data were segmented in two steps. First, the data were cut into three equal time periods, each containing ten ASRT blocks, to measure the temporal changes in error processing. Second, within each time period, response-locked ERPs were calculated, based on the correctness of the response (erroneous or correct) and the type of the given trial (pattern or random). Thus, altogether 3 × 2 × 2 segment types were created according to the periods, response correctness, and the trial types.

Following segmentation, an automatic artifact rejection method was applied (segments with activity above or below ± 100 μV were rejected), then, the artifact-free segments were baseline corrected based on the averaged pre-stimulus activity in the −200 to 0-ms time window. For erroneous pattern trials, the average number of artifact-free response-locked segments was 19.5 (SD = 7.3; $M_{\text{Period 1}}$ = 16.9, $SD_{\text{Period 1}}$ = 5.2, $M_{\text{Period 2}}$ = 21.1, $SD_{\text{Period 2}}$ = 9.5, $M_{\text{Period 3}}$ = 20.4, $SD_{\text{Period 3}}$ = 10.0). For erroneous random trials, this average was 19.5, as well (SD = 8.6; $M_{\text{Period 1}}$ = 20.3, $SD_{\text{Period 1}}$ = 7.8, $M_{\text{Period 2}}$ = 20.3, $SD_{\text{Period 2}}$ = 7.1, $M_{\text{Period 3}}$ = 18.1, $SD_{\text{Period 3}}$ = 6.8). The overall number of erroneous response-locked segments did not differ across trial types, $t(23) = -0.03$, $p = .975$. For correct pattern trials, the average number of artifact-free response-locked

segments was 366.1 (SD = 9.8; $M_{Period\ 1}$ = 367.1, $SD_{Period\ 1}$ = 9.9, $M_{Period\ 2}$ = 363.7, $SD_{Period\ 2}$ = 12.0, $M_{Period\ 3}$ = 367.5, $SD_{Period\ 3}$ = 6.7). For correct random trials, this average was 176.1 (SD = 12.3; $M_{Period\ 1}$ = 179.2, $SD_{Period\ 1}$ = 9.9, $M_{Period\ 2}$ = 171.7, $SD_{Period\ 2}$ = 13.6, $M_{Period\ 3}$ = 177.3, $SD_{Period\ 3}$ = 14.3). The overall number of correct response-locked segments was higher for pattern trials than for random trials, $t(23) = -88.48$, $p < .001$. Note that this difference partly originates from the fact that frequent random trials were excluded at the beginning of the analysis (see above), which decreased the number of artifact-free random segments. Segments were averaged for correct and erroneous responses, separately for pattern and random trials in each period.

Commonly, error commission is scarce and decreases over time in learning situations. However, it has been shown that as few as three to six EEG segments can yield reliable Ne and Pe effects (Meyer et al., 2013; Olvet & Hajcak, 2009; Pontifex et al., 2010). Therefore, it is plausible to calculate these components as markers of error processing in learning tasks, such as the present one. Consequently, the grand average ERPs calculated for the conditions detailed above were visually inspected, then, the observed and previously reported topographical distributions of the Ne and Pe components (Gehring et al., 1993) were considered. Accordingly, the Ne was quantified as the mean amplitude of the 0 to 100-ms time range relative to the erroneous response onset at electrode Cz, where this ERP component showed maximum amplitude. The Ne for correct responses was quantified in the same way as for erroneous responses. The Pe appeared earlier for correctly responded trials than for erroneous trials, therefore, its time window was chosen to match both response conditions. Accordingly, the Pe was quantified as the mean amplitude of the 100 to 300-ms time range relative to the erroneous as well as the correct response onset at electrode Cz. Erroneous minus correct difference waveforms were calculated for each ERP component, as well.

Data Analysis

In order to measure error processing during the online retrieval of probabilistic sequence knowledge, we focused on the trajectory of the responses to pattern trials. Therefore, behavioral and ERP data from pattern trials were analyzed in smaller time bins, each containing ten task blocks (i.e., periods, see also above). Data from the random trials were analyzed separately and according to the pattern trials; and, these data were used to indicate a retrieval-free baseline process, where incidental practice could happen. In terms of the behavioral data, for each participant, trial type, and period, median RTs for correct and erroneous responses as well as error ratios were calculated.

Behavioral measures (error ratios and RTs for correct and erroneous responses) for each trial types (pattern, random), respectively, were analyzed in repeated-measure analyses of variance (ANOVAs) with the factors Period (Period 1, 2, 3) and Trial type (pattern vs. random). ERP mean amplitudes for both components (Ne, Pe) were analyzed in repeated measures ANOVAs with the factors Response (erroneous vs. correct), Period (Period 1, 2, 3), and Trial type (pattern vs. random). Greenhouse-Geisser epsilon (ε) correction was used when necessary. Original df values and corrected p values (if applicable) are reported together with partial eta squared (η_p^2) as the measure of effect size. Bonferroni correction was used for pair-wise comparisons to correct for Type I error.

Results

Behavioral Results

Behavioral measures in the three periods are presented in Figure 2 separately for pattern and random trials.

Error ratio slightly varied across the time bins (main effect of Period: $F(2, 46) = 3.07$, $p = .056$, $\eta_p^2 = .12$; Period 1: 6.8%, Period 2: 7.9%, Period 3: 7.3%). Participants committed less errors on pattern trials than on random ones (significant main effect of Trial type: $F(1, 23) = 40.75$, $p < .001$, $\eta_p^2 = .64$; pattern trials: 4.9%, random trials: 9.8%). The significant Period × Trial type interaction, $F(2, 46) = 4.33$, $\varepsilon = .79$, $p = .028$, $\eta_p^2 = .16$, revealed that while error ratio on pattern trials did not change over time (Period 1: 5.2%, Period 2: 5.1%, Period 3: 4.5%; all ps ≥ .179), it increased on random trials (Period 1: 8.5%, Period 2: 10.8%, Period 3: 10.1%; Period 1 vs. Period 2: $p = .040$; Period 2 vs. Period 3: $p = .904$; Period 1 vs. Period 3: $p = .279$). The pattern – random difference did not change over the task (all ps ≥ .070), and participants were more accurate on pattern trials than on random ones in all periods (all ps < .001). Altogether, these results suggest that the online retrieval of the sequence knowledge could have helped participants to maintain accurate performance on pattern trials throughout the task, while performance was less consistent on the embedded baseline trials.

Correct RTs became faster with practice (significant main effect of Period: $F(2, 46) = 24.29$, $\varepsilon = .72$, $p < .001$, $\eta_p^2 = .51$; Period 1: 337 ms, Period 2: 316 ms, Period 3: 309 ms; Period 1 vs. Period 2: $p < .001$; Period 2 vs. Period 3: $p = .088$; Period 1 vs. Period 3: $p < .001$), and participants responded faster for pattern trials than for random ones (significant main effect of Trial type: $F(2, 46) = 63.43$, $p < .001$, $\eta_p^2 = .73$; pattern trials: 288 ms, random trials: 354 ms). These main effects were qualified by the

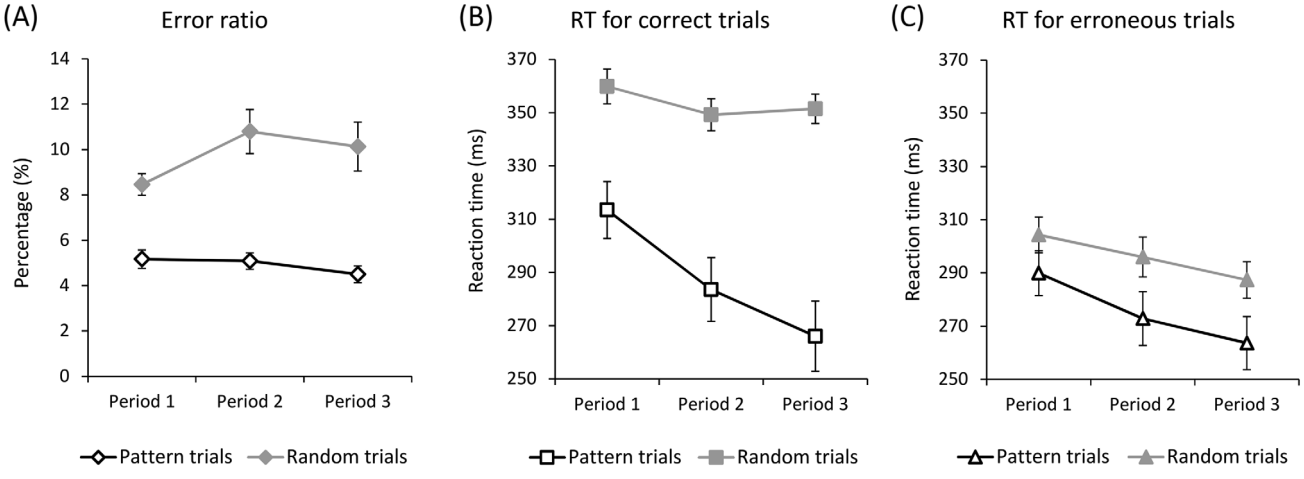

Figure 2. Group-average learning performance at the behavioral level. Black lines indicate perfromance on pattern trials and gray lines indicate performance on random trials. (A) Error ratio as a function of period (1–3, represented on the *X* axis). (B) Correct RTs as a function of period. (C) Erroneous RTs as a function of period. Error bars represent the standard error of mean.

significant Period × Trial type interaction, $F(2, 46) = 12.65$, $\varepsilon = .73$, $p < .001$, $\eta_p^2 = .36$. Pair-wise comparisons showed that the pattern – random difference increased as the task progressed (all *p*s < .001), and participants responded faster for pattern than for random trials in all periods (all *p*s < .001). Performance gradually improved on pattern trials (Period 1: 313 ms, Period 2: 284 ms, Period 3: 266 ms; all *p*s ≤ .022), while on random trials, this improvement was present only in the beginning of the task (Period 1: 360 ms, Period 2: 349 ms, Period 3: 351 ms; Period 1 vs. Period 2: $p = .001$; Period 2 vs. Period 3: $p = .719$; Period 1 vs. Period 3: $p = .015$). These results also reflect that sequence knowledge was acquired and retrieved online. Slight speed-up was observed on the embedded baseline trials, which, together with the increasing error ratio, suggests a moderate performance improvement, achieved incidentally throughout practice.

The analysis of *erroneous RTs* also revealed that erroneous responding became faster over time (significant main effect of Period: $F(2, 46) = 10.13$, $p < .001$, $\eta_p^2 = .31$; Period 1: 297 ms, Period 2: 284 ms, Period 3: 275 ms; Period 1 vs. Period 2: $p = .024$; Period 2 vs. Period 3: $p = .208$; Period 1 vs. Period 3: $p = .002$) and were overall faster for pattern trials than for random ones (significant main effect of Trial type: $F(1, 23) = 13.23$, $p = .001$, $\eta_p^2 = .36$; pattern trials: 275 ms, random trials: 296 ms). The Period × Trial type interaction was not significant, $F(2, 46) = 0.91$, $p = .410$, $\eta_p^2 = .04$, hence, the trajectory of erroneous RTs did not differ across trial types. In sum, participants committed errors faster on pattern trials, thus, this measure further reflects the effect of online sequence retrieval, opposing the moderate practice effect observed on the embedded baseline trials.

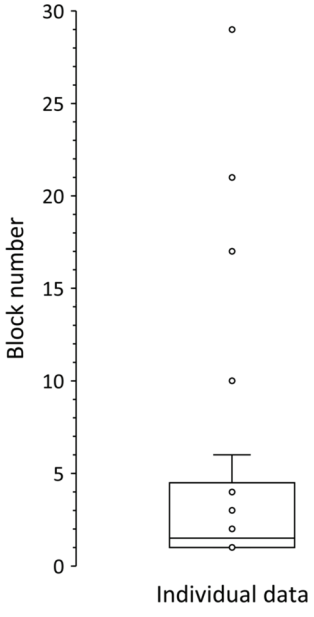

Figure 3. Boxplot indicating the discovery of the sequence based on the sequence report task. The *Y* axis represents the number of blocks (1–30). The box marks the interquartile range (i.e., the 50% of all values), the horizontal line marks the median value, the upper whisker marks the 25% of values above the interquartile range, and the dots mark individual values. Note that two participants are excluded here as indicated in the main text.

According to the sequence report, the discovery of the order of pattern trials emerged early in the task. Here, we excluded two participants who failed to provide at least 10 correct responses even after the final block of the task or reached this threshold during earlier blocks but failed to do so consistently in the remaining blocks. Participants consistently reported the repeating sequence from around the 5th block ($M = 5.0$, $SD = 7.1$, Figure 3).

Post-Error Behavioral Performance

To investigate whether adaptation is present and changes over time in the current experiment, post-error performance was tested, as well. The most common behavioral correlate of adaptation processes is the post-error slowing effect: Usually, RTs increase on the error-subsequent trials as a compensation (Simons, 2010). Thus, we compared RTs before and after an error have occurred (Dutilh, Van Ravenzwaaij, et al., 2012). First, we excluded errors that were immediately followed by another error, that is, only correct RTs were compared. Second, we calculated the median RTs for error-preceding and error-subsequent trials separately for pattern and random trials in each period. Third, these data were submitted to a 2 × 3 × 2 repeated-measure ANOVA with the factors Order (error-preceding vs. error-subsequent), Period (1, 2, 3), and Trial type (pattern vs. random). It is important to note that due to the sequence – random alteration in the task, an inevitable confound is present in the dataset: If an error occurs on a pattern trial, two random trials are compared in the present analysis and vice versa.

The significant main effect of Order confirmed the presence of the post-error slowing effect, $F(1, 23) = 40.30$, e = .74, $p < .001$, $\eta_p^2 = .64$: Participants responded 40 ms (SD = 54 ms) slower after than before error commission. The main effect of Period, $F(2, 46) = 6.80$, $p = .007$, $\eta_p^2 = .23$, and the main effect of Trial type, $F(1, 23) = 9.12$, $p = .006$, $\eta_p^2 = .28$, were also significant, reflecting the above-described general speed-up and pattern vs. random difference, respectively. The significant Order × Period interaction, $F(2, 46) = 4.76$, $p = .013$, $\eta_p^2 = .17$, qualified the main effects. Pair-wise comparisons showed that the difference between error-preceding and error-subsequent RTs decreased over time (Period 1 = 51 ms; Period 2 = 47 ms; Period 3 = 23 ms; Period 1 vs. Period 2: $p = .749$, Period 2 vs. Period 3: $p = .006$, Period 1 vs. Period 3: $p = .011$). Error-subsequent RTs were slower than error-preceding RTs in all periods (all $ps \leq .003$). Moreover, while error-preceding RTs decreased from Period 1 to Period 2 ($p = .013$; Period 1 = 324 ms, Period 2 = 293 ms, Period 3 = 290 ms; all other $ps \geq .107$), error-subsequent RTs decreased throughout the task (Period 1 = 374 ms; Period 2 = 340 ms; Period 3 = 312 ms; Period 1 vs. Period 2: $p = .015$; Period 2 vs. Period 3: $p = .341$; Period 1 vs. Period 3: $p = .001$). The Order × Trial type, the Period × Trial type, and the Order × Period × Trial type interactions were not significant, $F(2, 46) = 2.75$, $p = .111$, $\eta_p^2 = .11$, $F(2, 46) = 0.34$, $p = .714$, $\eta_p^2 = .02$, $F(2, 46) = 0.92$ $p = .406$, $\eta_p^2 = .04$, respectively. Overall, the post-error slowing effect decreased over time similarly for pattern and random trials.

ERP Results

Grand average ERP waveforms for erroneous and correct responses as well as for their difference are presented in Figures 4 and 5, separately for pattern and random trials in each period at electrode Cz. For erroneous responses, the Ne appeared as a sharp negative wave followed by the Pe as a broad positive wave. For the correct responses, the corresponding ERP waveforms were attenuated. In addition, while the Ne for correct responses appeared as a relative negativity with similar latency (with a peak around ca. 40 ms) as for the erroneous responses, the Pe for correct responses occurred earlier (with a peak around ca. 120 ms) than for the erroneous ones and returned to baseline around 200 ms (cf. Ferdinand et al., 2008). Means and standard deviations of each ERP component in each period split by trial type are presented in Table 1. The ERP data were analyzed in 2 × 3 × 2 repeated-measure ANOVAs with the factors Response (erroneous vs. correct), Period (1, 2, 3), and Trial type (pattern vs. random). Only the significant effects are reported here; the summary of all effects is presented in Table 2.

The analysis of the *Ne* yielded a significant main effect of Response, $F(1, 23) = 49.71$, $p < .001$, $\eta_p^2 = .68$: Erroneous responses elicited a larger (more negative) Ne than correct responses. The main effect of Period also appeared to be significant, $F(2, 46) = 19.16$, $\varepsilon = .73$, $p < .001$, $\eta_p^2 = .45$, revealing a gradually decreasing Ne regardless of response type and trial type (all $ps \leq .013$). These main effects were qualified by the Response × Period interaction, $F(2, 46) = 5.87$, $p = .005$, $\eta_p^2 = .20$. Pairwise comparisons showed that although the Ne for erroneous responses was larger than the Ne for correct responses in every period (all $ps < .001$), the erroneous – correct difference of the trial-unspecific Ne (i.e., Ne irrespective of trial type) decreased from Period 1 to Period 3 ($p = .004$; Period 1 vs. Period 2: $p = .130$; Period 2 vs. Period 3: $p = .065$). The Ne for erroneous responses significantly decreased throughout the task (all $ps \leq .022$). In contrast, the Ne for correct responses decreased only from Period 1 to Period 2 ($p = .042$), while it did not change for the remainder of the task (Period 2 vs. Period 3: $p = .999$; Period 1 vs. Period 3: $p = .079$). We did not find any significant effects involving the factor Trial type (Tables 1 and 2). In sum, the Ne decreased for erroneous and correct responses over time, regardless of trial type (Figures 4 and 5).

The analysis of the *Pe* yielded a significant main effect of Response, $F(1, 23) = 12.60$, $p = .002$, $\eta_p^2 = .35$, reflecting a larger Pe for erroneous responses than for correct responses. The main effect of Period also appeared to be significant, $F(2, 46) = 22.04$, $\varepsilon = .75$, $p < .001$, $\eta_p^2 = .49$, revealing a gradually increasing Pe, regardless of response

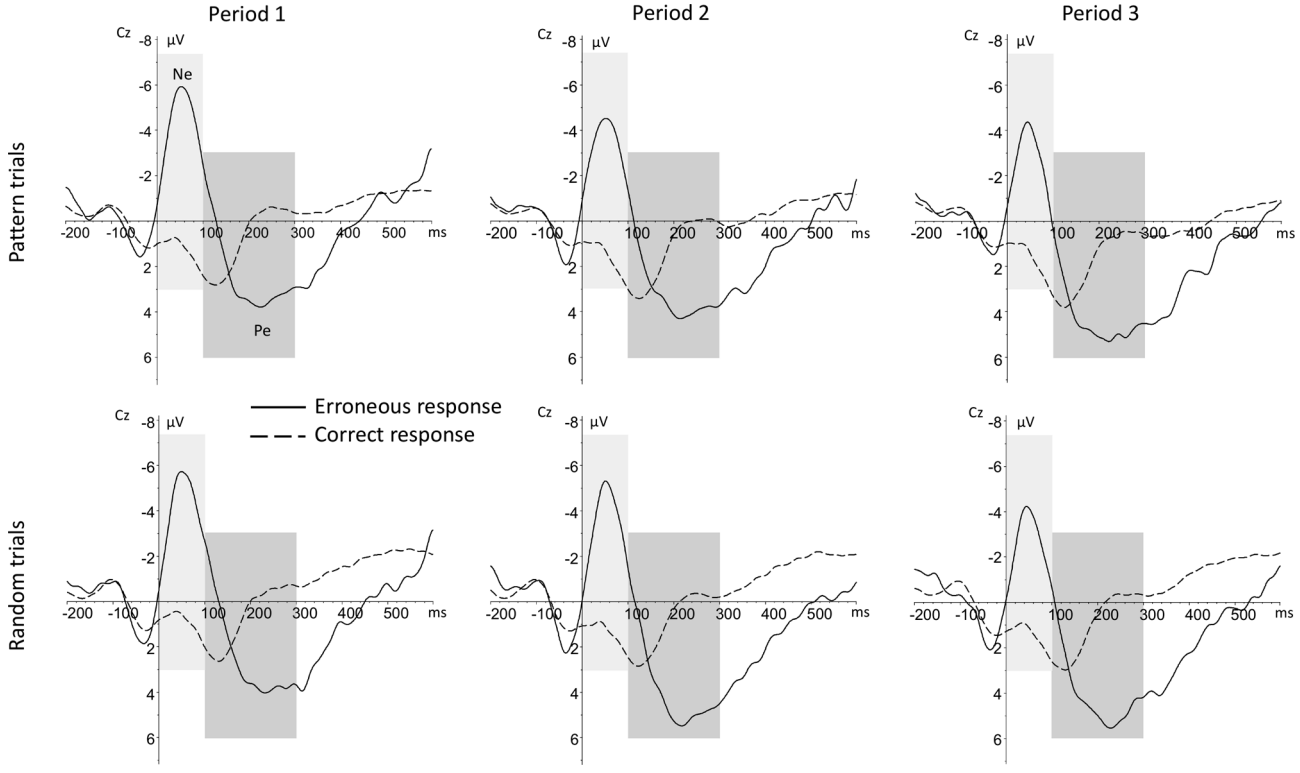

Figure 4. Grand average ERP waveforms synchronized to the response onset at electrode Cz displaying Ne and Pe components separately for the three periods, two response types, and two trial types. Note that negativity is plotted upwards here and in the following figures. Solid lines denote erroneous response-locked waveforms and dashed lines denote correct response-locked waveforms. Light gray shading indicates the time window where the Ne was measured, while dark gray shading indicates the time window of the Pe. Rows mark the two trials types and columns mark the three periods.

type and trial type (all $ps \leq .010$). These main effects were further qualified by the significant Response × Period interaction, $F(2, 46) = 5.81$, $p = .006$, $\eta_p^2 = .20$. Pairwise comparisons showed that although the Pe was larger for erroneous responses than for correct responses in all periods (all $ps \leq .016$), the erroneous – correct difference of the trial-unspecific Pe increased from Period 1 to Period 2 ($p = .036$; Period 2 vs. Period 3: $p = .122$; Period 1 vs. Period 3: $p = .009$). In addition, the Pe for erroneous responses significantly increased throughout the task (all $ps \leq .018$). In contrast, the Pe for correct responses increased only from Period 1 to Period 2 ($p = .047$), while it did not show further changes (Period 2 vs. Period 3: $p = .429$; Period 1 vs. Period 3: $p = .013$). Opposing the Ne, the Period × Trial type interaction reached significance, as well, $F(2, 46) = 3.67$, $p = .033$, $\eta_p^2 = .14$. Pair-wise comparisons showed that the difference of the response-unspecific Pe (i.e., Pe irrespective of response correctness) between pattern and random trials increased by the end of the task (Period 1 vs. Period 2: $p = .368$; Period 2 vs. Period 3: $p = .039$; Period 1 vs. Period 3: $p = .062$). Particularly, the Pe was larger for pattern trials than for random ones in Period 3 ($p = .045$, all other $ps \geq .506$). The Pe for pattern trials gradually increased as the task progressed (all $ps \leq .029$), while the Pe for random trials increased only from Period 1 to Period 2 ($p < .001$; Period 2 vs. Period 3: $p = .999$; Period 1 to Period 3: $p = .005$). Altogether, regardless of trial type, the Pe for erroneous responses gradually increased, while this increase was modest for the correct responses. Regardless of response correctness, a larger Pe was observed for pattern trials than for random ones in the end of the task (Figures 4 and 5).

Possible Distortion Effects in the Ne: Stimulus-Locked ERPs

It has been previously raised that overlapping ERPs may lead to different distortion effects in experiments where RTs vary across conditions, as in the present one (Coles, Scheffers, & Holroyd, 2001). Therefore, we investigated the stimulus-locked P3 component, as well. To this end, EEG segments were extracted from −200 ms to 600 ms relative to stimulus onset; then, these were averaged for each period and trial type (see also the analyses of Kóbor et al., 2018). For the sake of completeness and to match the main analyses, besides correctly responded stimuli, erroneously responded stimuli were also investigated.

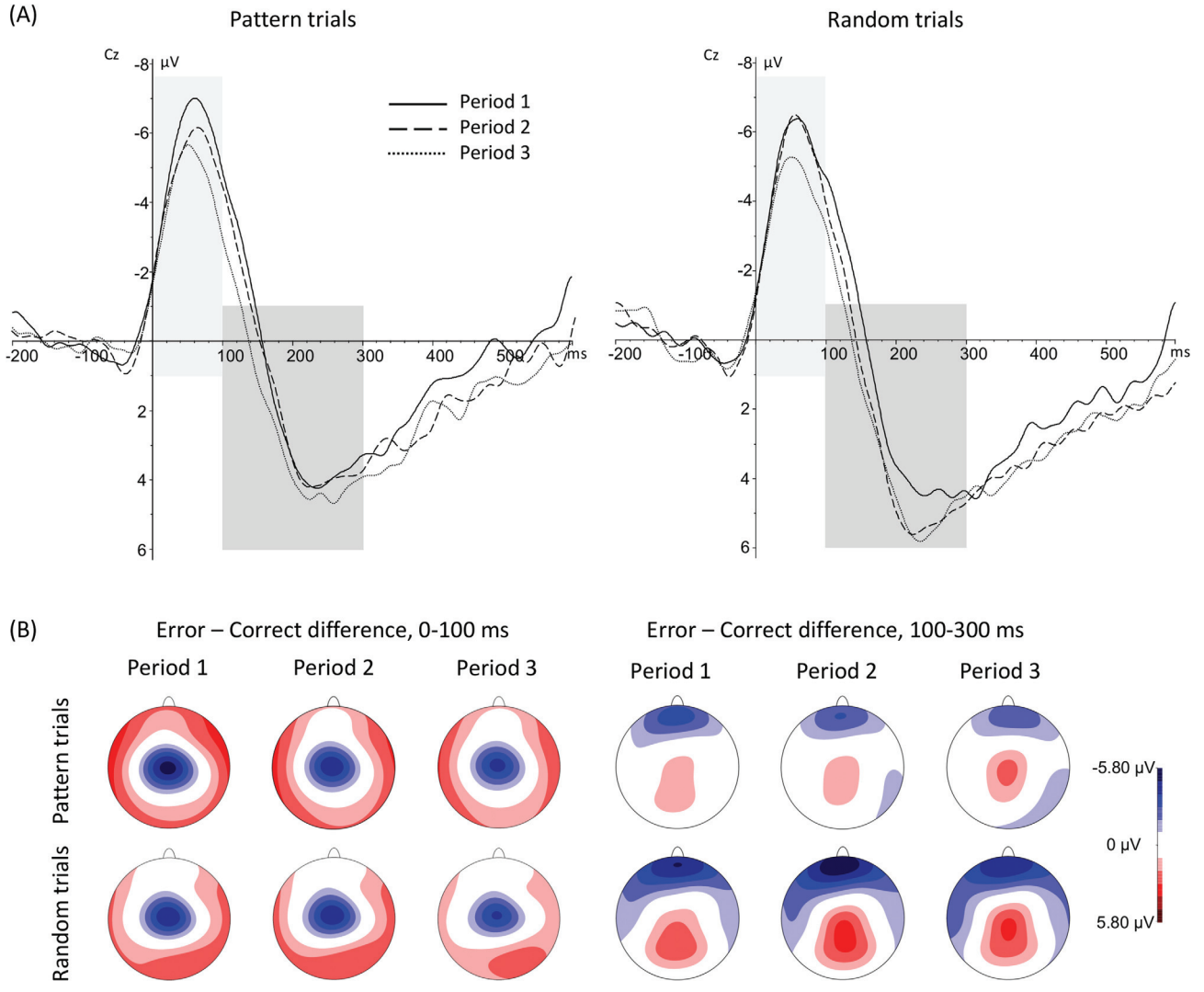

Figure 5. (A) Erroneous minus correct difference waveforms at electrode Cz, separately for pattern and random trials. Solid lines denote Period 1, dashed lines denote Period 2, and dotted lines denote Period 3. Light gray shading indicates the time window of Ne, while dark gray shading indicates the time window of Pe. (B) The scalp topography (amplitude distribution) of the erroneous – correct difference in the time windows of the Ne (0–100 ms) and the Pe (100–300 ms), respectively, separately for pattern and random trials.

Table 1. Sample means (*M*) and standard deviations (*SD*) of Ne and Pe components, separately for each response type (erroneous or correct), period, and trial type (pattern or random)

	Ne for erroneous responses	Ne for correct responses	Pe for erroneous responses	Pe for correct responses
	M (*SD*) μV	*M* (*SD*) μV	*M* (*SD*) μV	*M* (*SD*) μV
		Pattern trials		
Period 1	−4.3 (3.22)	1.2 (1.74)	2.4 (2.76)	0.8 (2.27)
Period 2	−3.3 (2.86)	1.6 (1.82)	3.1 (2.84)	1.3 (2.81)
Period 3	−2.7 (2.83)	1.7 (1.96)	4.3 (2.74)	1.8 (2.51)
		Random trials		
Period 1	−4.1 (3.25)	0.9 (2.15)	2.4 (2.89)	0.7 (2.36)
Period 2	−3.5 (3.68)	1.4 (2.30)	3.8 (2.57)	0.9 (2.77)
Period 3	−2.7 (3.24)	1.4 (2.24)	4.1 (2.73)	1.0 (2.72)

The P3 was quantified as the mean amplitude between 250 ms and 350 ms at electrode Pz, where this component appeared with maximum amplitude. Grand average stimulus-locked ERP waveforms displaying the P3 component are presented in Figure 6. Please, note that the P3 for erroneously responded stimuli were calculated from

Table 2. Summary of results from ANOVAs performed on the ERP data

		Effect						
ERP component	Statistics	Response	Period	Trial Type	Response × Period	Response × Trial Type	Period × Trial Type	Response × Period × Trial Type
Ne	*F*	49.71	19.16	0.51	5.87	0.54	0.09	0.47
	p	**< .001**	**< .001**	.484	**.005**	.471	.914	.628
	η_p^2	.684	.454	.022	.203	.023	.004	.020
Pe	*F*	12.60	22.04	0.68	5.81	2.48	3.67	1.10
	p	**.002**	**< .001**	.417	**.006**	.129	**.033**	.341
	η_p^2	.354	.489	.029	.202	.097	.138	.046

Note. *p*-values below .050 are boldfaced.

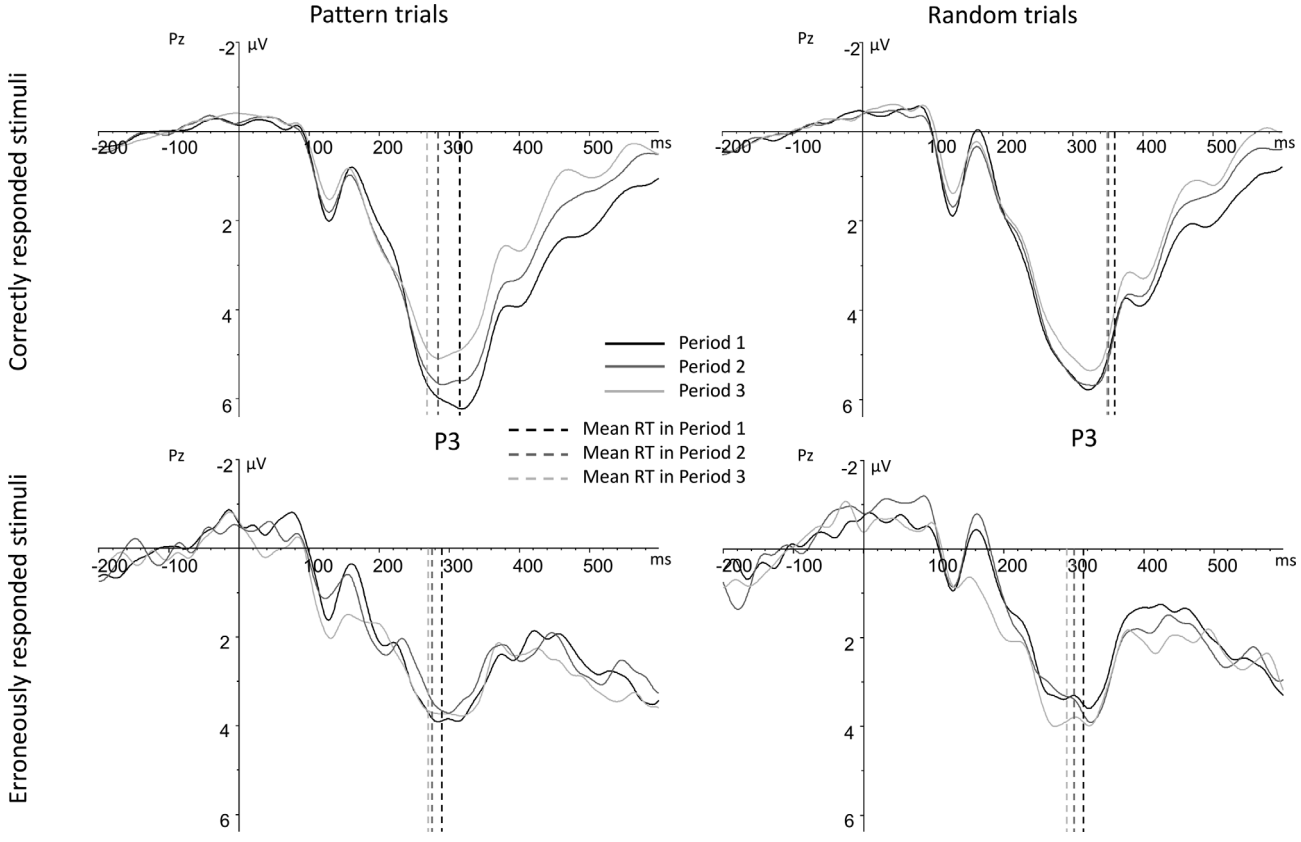

Figure 6. Grand average ERP waveforms synchronized to stimulus onset at electrode Pz displaying the P3 component time-locked to the correctly responded trials (upper panel) and time-locked to the erroneously responded trials (lower panel) separately for the two trial types (pattern vs. random, left and right panels, respectively). Black lines indicate the first period, dark gray lines indicate the second period, and light gray lines indicate the third period. Dashed vertical lines show the average RT observed for the given trial and response type in the given period. Colors are used according to the ERP waveforms. Note that the P3 for erroneously responded trials is noisy due to the low number of segments available.

less than the adequate number of segments, thus, the resulting waveform was noisy. The mean amplitude of the P3 was analyzed in a 2 × 3 × 2 repeated measures ANOVA with the factors Response (erroneous vs. correct), Period (1, 2, 3), and Trial type (pattern vs. random).

The P3 for erroneously responded stimuli was reduced compared with the correctly responded ones (significant main effect of Response: $F(1, 23) = 81.41$, $p < .001$, $\eta_p^2 = .78$). The main effect of Period, $F(2, 46) = 1.66$, $p = .201$, $\eta_p^2 = .07$, and the main effect of Trial Type, $F(1, 23) = 0.42$, $p = .523$, $\eta_p^2 = .02$, did not reach significance. The significant Response × Period interaction, $F(2, 46) = 4.99$, $p = .011$, $\eta_p^2 = .18$, revealed that although the P3 for erroneously responded stimuli was lower than the P3 for correctly responded stimuli in all periods (all *p*s < .001), the erroneous – correct difference of the trial-unspecific P3 decreased from Period 1 to Period 3 ($p = .033$, all other *p*s ≥ .206). The P3 for correctly responded stimuli

decreased (Period 1 vs. Period 2: $p = .602$, Period 2 vs. Period 3: $p = .003$, Period 1 vs. Period 3: $p < .001$), while the P3 for erroneously responded stimuli did not change over time (all ps = .999). The Period × Trial type interaction appeared as significant, as well, $F(2, 46) = 6.06$, $p = .010$, $\eta_p^2 = .18$, revealing that while the response-unspecific P3 did not differ across trial types in any of the periods (all ps $\geq .057$), the pattern – random difference decreased from Period 1 to Period 3 ($p = .028$, all other ps $\geq .107$), particularly, the P3 for pattern stimuli decreased in the late phase of the task (Period 1 vs. Period 3: $p = .045$, Period 1 vs. 2: $p = .880$, Period 2 vs. Period 3: $p = .147$), while the P3 for random stimuli did not change (all ps = .999, see Figure 6). The Response × Trial type interaction and the Response × Period × Trial type interaction were not significant, $F(2, 46) = 0.73$, $p = .401$, $\eta_p^2 = .03$; $F(2, 46) = 0.38$, $p = .684$, $\eta_p^2 = .16$, respectively. That is, the temporal change of the P3 component differed according to the correct – error contrast and the pattern – random contrast, respectively.

We visually inspected the temporal relationship of the P3 component and the average RTs across response types and trial types. The average RT fell into the peak of the P3 in most cases, except for correctly responded random stimuli (Figure 6). Meanwhile, we did not find any trial type-related effect in the Ne data (Table 2, Figures 4 and 5). Therefore, although the P3 component and correct RTs vary across trial types as a function of task period, the response-locked activity does not seem to be contaminated with or distorted by the stimulus-locked ERP activity.

Discussion

In the present study, we investigated error processing during the intentional retrieval of probabilistic sequence knowledge. To seize the temporal characteristics of error processing, we divided the task into three equal time periods. By using stimuli with different physical characteristics and providing different instructions, the initial acquisition and online retrieval of the repeating events of a probabilistic sequence has been detached from an embedded baseline process provided by practice on the infrequent random events. The sequence reports proved that knowledge of the repeating sequence was explicitly available early in the task. Further performance improvement was observed on the repeating events throughout the task, opposing the random ones. It is presumable that the former process has been grounded by the already existing sequence knowledge and reflected retrieval processes as participants aimed to achieve better performance on the task. While accuracy decreased for random trials, RTs became slightly faster, supporting our expectations of a retrieval-free baseline process where incidental RT improvement can happen. The post-error slowing effect decreased over time comparably for the sequence retrieval and the baseline process, reflecting a sequence-independent reduction in behavioral adjustments.

Automatic detection and conscious evaluation of the committed errors were indicated by the presence of Ne and Pe ERP components, respectively. Correct response-related components were considered to control for correct-response related processes. The stimulus-locked P3 was investigated, as well, to exclude the possibility of distortion effects in the Ne caused by the varying stimulus-locked ERPs and RTs across conditions. Surprisingly, the Ne for erroneous responses as well as the response-unspecific Ne decreased over time, comparably for the sequence retrieval and the embedded baseline process. The trial-unspecific Pe for erroneous responses gradually increased over time, while the trial-unspecific Pe for correct responses showed a moderate increase only, similarly across the retrieved sequence and the random trials. The response-unspecific Pe appeared to be larger for pattern than for random trials by the end of the task. Altogether, we show evidence that both automatic error detection and conscious error evaluation are sensitive to general performance improvement in the task, while neither the Ne nor the Pe is selectively sensitive to sequence retrieval.

The analyses of the Ne yielded two main results: First, the Ne continuously decreased over time, as opposed to our hypothesis based on the main theoretical accounts of the Ne. We propose that instead of the effect of sequence learning and retrieval, the Ne amplitude modulation reflects a general adaptation to the task. It is presumable that as participants practiced the task, the mapping of the stimuli and the corresponding responses (S–R mappings) became automatized. The automatization of S–R mappings was also reflected by the stimulus-locked P3 data (cf. Kóbor et al., 2019; Verleger, 1997; Verleger, Jaśkowski, & Wascher, 2005; Verleger, Metzner, Ouyang, Śmigasiewicz, & Zhou, 2014): The trial-unspecific P3 amplitude for correctly responded stimuli decreased over time, whereas the trial-unspecific P3 amplitude for the erroneously responded stimuli did not change. Moreover, post-error slowing also decreased throughout the task, suggesting that less adjustment was needed after an error occurred as participants proceeded with the task (Danielmeier & Ullsperger, 2011; Dutilh, Vandekerckhove, et al., 2012). Altogether, the automatization of S–R mappings could have supported the automatic detection of errors, resulting in a decreasing Ne. Second, the Ne did not show sensitivity to the predictability of the sequence. Likewise, post-error adjustment took place comparably for the retrieved sequence and the

embedded baseline process. These results support the notion that the Ne as well as the S–R mappings created throughout the task are independent of sequence learning and retrieval processes.

These observations are in line with the *error detection/mismatch theory* (Bernstein et al., 1995; Falkenstein et al., 1991; Gehring et al., 1993): The comparison of erroneous and correct response representations could have required less resources as S–R mappings became automatized, which was reflected in the Ne decrease. The *motivational significance theory* (Gehring et al., 1993; Hajcak et al., 2005) can also explain the observed Ne decrease. It has been previously shown that errors violating task goals (e.g., flanker-related errors in the Eriksen flanker task) elicit a greater Ne than errors originating from mere response confusion (e.g., non-flanker errors), suggesting that performance-related significance modulates the magnitude of the Ne (Maier, Di Pellegrino, & Steinhauser, 2012; Maier & Steinhauser, 2016). Furthermore, adjustments in post-error adaptation also reflect the changes in error significance (Maier, Yeung, & Steinhauser, 2011). Particularly, errors should imply the possibility of learning to adaptively use them, meaning that post-error adaptation might not occur (or might decrease in amount) if the significance of errors becomes low. In the present study, we, indeed, observed a decreasing post-error slowing effect that might have indicated a decrease in error significance as the task progressed. This explanation could be in line with the study of Holroyd, Krigolson, Baker, Lee, and Gibson (2009) showing that the amplitude of the feedback-related negativity is modulated by adaptation processes. Similarly, we assume that the significance of errors could have reduced as responding became automatized. Additionally, the rapid acquisition of sequence knowledge, that is, the completion of participants' main task goal, could have also led to a drop of error significance, finally resulting in an Ne decrease. Nevertheless, as error significance was not directly manipulated or measured in the present experiment, this explanation has to be treated with caution.

To this date, studies investigating the neurophysiological aspect of error processing in the intentional acquisition of repeating regularities focused on the initial learning processes. Here, we go beyond these studies by describing the Ne as well as the Pe during the continuous use of sequence knowledge to improve task performance. Prior studies revealed no sequence-specific modulations of the Ne (Ferdinand et al., 2008; Rüsseler et al., 2003), except when the development of knowledge was examined across smaller time bins, where the Ne increased with sequence learning compared with the random stimulus stream (Rüsseler et al., 2018). Yet, these studies used deterministic sequences, as opposed to the probabilistic nature of the present stimulus stream. In our experiment, the Ne amplitude modulation appeared similarly for the repeating sequence and the random elements. This result is contradictory to those found in the study of Rüsseler et al. (2018); however, it is presumable that while erring has a high cost during the development of representations, especially for deterministic regularities, it has less impact once the representations and S–R mappings are strengthened.

The Pe for erroneous responses, on the one hand, increased throughout the task, irrespective of the predictability of the sequence. Although we expected an increase selectively for pattern trials, the obtained results can be still explained by the theoretical approaches of the Pe. The *error awareness approach* claims that the magnitude of the Pe reflects the level of awareness regarding the committed error (Endrass et al., 2007; Nieuwenhuis et al., 2001): The higher the level of error awareness, the larger the Pe. The *account of P3b* states that the Pe is a P3- or P3b-like component and reflects the salience of an error (Falkenstein et al., 1991; Overbeek et al., 2005; Ridderinkhof et al., 2009), that is, a higher relevance or saliency of an error yields a larger Pe. Finally, the *account of decision evidence accumulation* hypothesizes that the Pe reflects the level of confidence in or the amount of evidence available for the omitted error (Boldt & Yeung, 2015; Steinhauser & Yeung, 2012). Although these frameworks assume different functional significance of the Pe, all can explain the observed increase: As participants practiced the task and the S–R mappings strengthened, awareness regarding the representation of errors could have increased, errors could have become more salient for conscious evaluation, and error confidence could have increased, as well.

On the other hand, the response-unspecific Pe was larger for the retrieved sequence compared with the embedded random events by the end of the task. The above described theories can explain this effect, as well: As pattern trials are more salient in the present task, it is presumable that errors on these trials are characterized with higher error awareness and more evidence for error commission. Previously, only one study investigated the Pe as the correlate of error awareness in the acquisition of repeating regularities, to our knowledge: Ferdinand et al. (2008) did not observe any sequence-specific modulation of the component. This result is opposing the present study. We assume that while the sequence knowledge had been explicitly acquired already by the first period in the present experiment, Ferdinand et al. (2008) measured developing representations, leading to different results. We suggest that the Pe for erroneous responses is not sensitive to the predictability of the sequence in the present study. Meanwhile, when the combined processing of correct and erroneous responses is measured, sensitivity to the sequence can be observed in terms of conscious evaluation, at least by the end of the

task, suggesting that conscious response evaluation could be supported by the retrieval processes.

In conclusion, the present study adds further relevant results to the field, as, to the best of our knowledge, this is the first study investigating the neurophysiological correlates of error processing during the online retrieval of sequence knowledge in a probabilistic environment. The observed Ne effects indicate that adaptation to the environment based on the development of S–R mappings results in a rapid amplitude drop. Likewise, the observed Pe effects indicate that error awareness is also supported by adaptation processes. As neither the Ne nor the Pe is modulated differently as a function of sequence predictability, we suggest that automatic error detection and conscious error evaluation are independent of sequence learning and retrieval. Finally, we propose that the investigation of the Ne and the Pe in the case of automatic behaviors should be further extended.

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History
Received March 16, 2019
Accepted February 10, 2020
Published online May 7, 2020

Acknowledgements
This research was supported by the National Brain Research Program (project 2017-1.2.1-NKP-2017-00002, PI: Dezso Nemeth); the Hungarian Scientific Research Fund (OTKA FK 124412, PI: Andrea Kóbor, OTKA PD 124148, PI: Karolina Janacsek, OTKA K 128016, PI: Dezso Nemeth); the IDEXLYON Fellowship of the University of Lyon as part of the Programme Investissements d'Avenir (ANR-16-IDEX-0005 to Dezso Nemeth); the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (to Andrea Kóbor and Karolina Janacsek); and the ÚNKP-19-3 New National Excellence Program of the Ministry for Innovation and Technology (to Kata Horváth). The authors thank the help of Emese Várkonyi, Csenge Török, and Noémi Éltető in data acquisition.

Conflict of Interest
The authors do not have any actual or potential conflicts of interest.

Authorship
Kata Horváth analyzed data and wrote the manuscript; Zsófia Kardos designed the experiment, supervised data analysis, and

wrote the manuscript, Ádám Takács designed the experiment, supervised data analysis, and wrote the manuscript; Valéria Csépe provided intellectual support and wrote the manuscript; Dezso Nemeth designed and supervised the experiment, provided financial and intellectual support, and wrote the manuscript; Karolina Janacsek designed the experiment, supervised data analysis, and wrote the manuscript; Andrea Kóbor designed and supervised the experiment, analyzed data, supervised data analysis, and wrote the manuscript.

Open Data

There are no linked research datasets for this submission because data will be made available on request.

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VI. Study 2: When and to what degree can we adjust automatic behaviours when the environment becomes unpredictable without any noticeable change at the surface level?

Publication:

Kóbor, A., **Horváth, K.**, Kardos, Z., Nemeth, D., & Janacsek, K. (2020). Perceiving structure in unstructured stimuli: Implicitly acquired prior knowledge impacts the processing of unpredictable transitional probabilities. Cognition, 205, 104413.

The **Supplementary Material** for the publication can be found in Appendix II.

Cognition 205 (2020) 104413

Contents lists available at ScienceDirect

Cognition

journal homepage: www.elsevier.com/locate/cognit

Perceiving structure in unstructured stimuli: Implicitly acquired prior knowledge impacts the processing of unpredictable transitional probabilities

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ARTICLE INFO

Keywords:
Implicit statistical learning
Persistence
Prior knowledge
Randomness
Transitional probabilities

ABSTRACT

It is unclear how implicit prior knowledge is involved and remains persistent in the extraction of the statistical structure underlying sensory input. Therefore, this study investigated whether the implicit knowledge of second-order transitional probabilities characterizing a stream of visual stimuli impacts the processing of unpredictable transitional probabilities embedded in a similar input stream. Young adults ($N = 50$) performed a four-choice reaction time (RT) task that consisted of structured and unstructured blocks. In the structured blocks, more probable and less probable short-range nonadjacent transitional probabilities were present. In the unstructured blocks, the unique combinations of the short-range transitional probabilities occurred with equal probability; therefore, they were unpredictable. All task blocks were visually identical at the surface level. While one-half of the participants completed the structured blocks first followed by the unstructured blocks, this was reversed in the other half of them. The change in the structure was not explicitly denoted, and no feedback was provided on the correctness of each response. Participants completing the structured blocks first showed faster RTs to more probable than to less probable short-range transitional probabilities in both the structured and unstructured blocks, indicating the persistent effect of prior knowledge. However, after extended exposure to the unstructured blocks, they updated this prior knowledge. Participants completing the unstructured blocks first showed the RT difference only in the structured blocks, which was not constrained by the preceding exposure to unpredictable stimuli. The results altogether suggest that implicitly acquired prior knowledge of predictable stimuli influences the processing of subsequent unpredictable stimuli. Updating this prior knowledge seems to require a longer stretch of time than its initial acquisition.

1. Introduction

Acquiring implicit knowledge of the statistical structure organizing environmental events is crucial for many cognitive functions and contributes to the automatization of behaviors (Armstrong, Frost, & Christiansen, 2017; Aslin, 2017; Kaufman et al., 2010; Maheu, Dehaene, & Meyniel, 2019). This ability involves not only the mere extraction of various statistical structures but also the efficient use of the acquired implicit knowledge across situations that differ in specific features at the surface level but share common features at the structural level. In everyday life, if conditions are substantially similar, we usually learn fast how to use the updated versions of applications or operating

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https://doi.org/10.1016/j.cognition.2020.104413
Received 16 August 2019; Received in revised form 14 July 2020; Accepted 16 July 2020
Available online 31 July 2020

systems without checking manuals, running online searches, or even consciously accessing the course of our actions by using previous experiences. However, the potential stability of the already acquired implicit knowledge when applied in similar situations has not been completely elucidated (Bulgarelli & Weiss, 2016; Conway, 2020; R. Frost, Armstrong, & Christiansen, 2019). Therefore, we investigate the stability of implicit knowledge of a statistical structure underlying a stream of visual stimuli that remains the same at the surface level but, in time, becomes unpredictable at the structural level.

According to the broad frameworks of cognitive processing, learning, and decision making, the processing of new information and the formation of expectations about future events are guided by inferences based on prior experiences (e.g., Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Friston, 2005; Friston, 2010; Friston, Stephan, Montague, & Dolan, 2014; Griffiths, Kemp, & Tenenbaum, 2008; Shohamy & Daw, 2015). This also pertains to randomness perception (Hahn & Warren, 2009; Sun et al., 2015; Sun & Wang, 2010; Teigen & Keren, 2020; Warren, Gostoli, Farmer, El-Deredy, & Hahn, 2018), binary choice behavior (Feher da Silva & Baldo, 2012; Gaissmaier & Schooler, 2008; James & Koehler, 2011) as well as implicit statistical learning (Conway, 2020; Qian, Jaeger, & Aslin, 2012). The persistence of the primarily learned statistical structure and its influence on further processing have been evidenced by behavioral (e.g., Bulgarelli & Weiss, 2016; Gebhart, Aslin, & Newport, 2009; Lany, Gómez, & Gerken, 2007) as well as neurocognitive measures (e.g., Honbolygó & Csépe, 2013; Karuza et al., 2016; Mullens et al., 2014; Todd, Frost, Fitzgerald, & Winkler, 2020; Todd, Provost, & Cooper, 2011). However, statistical structures can differ in characteristics and complexity (Conway, 2020), and multiple statistical structures can be acquired even from the same stimulus sequence (Conway & Christiansen, 2001; Daltrozzo & Conway, 2014; Frost et al., 2019; Kóbor et al., 2018; Simor et al., 2019).

According to the model proposed by Meyniel, Maheu, and Dehaene (2016), instead of simpler statistics such as frequencies and alternations of events, the computation of time-varying, non-stationary, local transitional probabilities between consecutive events could be considered as the "building block" of implicit statistical learning and knowledge (see also Maheu et al., 2019; Orbán, Fiser, Aslin, & Lengyel, 2008). Humans have been found to be highly proficient in extracting even the nonadjacent transitional probabilities, referring to predictive relations between elements of a sequence that includes ordered stimuli interspersed with random ones (Conway, 2020; Frost & Monaghan, 2016; Malassis, Rey, & Fagot, 2018; Mueller, Milne, & Männel, 2018; Rey, Minier, Malassis, Bogaerts, & Fagot, 2018).

Using transitional probabilities in a series of experiments, Gebhart et al. (2009) changed the underlying statistical structure of stimuli in the middle of an auditory statistical learning task. They successively presented two different but overlapping artificial speech streams composed of trisyllabic nonsense words characterized by transitional probabilities. In this way, the surface of the stimuli remained similar throughout the task while their structure changed. If the change was not explicitly signaled or the second structure was not presented for a tripled duration, participants only learned the first structure. This indicated that the primarily experienced structure limited the capacity to acquire the successive structure. However, in this study, a certain statistical structure determined by transitional probabilities was always present during the task (see also Bulgarelli & Weiss, 2016; Weiss, Gerfen, & Mitchel, 2009; Zinszer & Weiss, 2013). Therefore, it is unclear whether the results would have been the same if the statistical structure per se had been eliminated. For instance, it could be clarified whether changing only the predictability of the same nonadjacent transitional probabilities over the course of learning influences their later extraction.

Furthermore, in the study by Gebhart et al. (2009), after exposure to the speech stream, knowledge of the statistical structures was measured with two-alternative forced-choice test trials in which familiarity judgments were provided. Meanwhile, processing-based or "online" tasks should be favored, since these tasks more likely reflect implicitly acquired statistical knowledge about which no consciously accessible representations are available. These tasks could also capture the trajectory of acquisition and provide information about the stability of the underlying processes when these processes actually operate (Christiansen, 2018; Frost et al., 2019). Therefore, it remains to be tested with an online, unsupervised statistical learning task (Fiser & Aslin, 2001; Qian et al., 2012) how changing the predictability of nonadjacent transitional probabilities impacts further acquisition.

Consequently, in the present study, we used a four-choice reaction time (RT) task to online measure the implicit processing and acquisition of a sequence composed of second-order nonadjacent transitional probabilities. In this sequence, elements in position $n - 2$ predicted elements in position n with high or low probability. Unknown to participants, half of the task blocks included an alternating regularity between nonadjacent trials, yielding more probable and less probable short-range transitional probabilities (see Fig. 1). The short-range transitional probabilities were three successive trials, hereafter referred to as triplets. In the other half of the task blocks, the alternating regularity was absent, and unique triplets appeared with equal probability. The task blocks were labeled as structured and unstructured blocks, according to the presence or absence of the alternating regularity. By creating either biased (high or low) or equal probabilities of triplets, stimuli were predictable in the structured blocks and unpredictable in the unstructured blocks. With this design, it could be tested how prior knowledge of the predictability of triplets influences their processing when predictability changes from the first to the second half of the task. To this end, while one-half of the fifty participants completed the structured blocks first followed by the unstructured blocks, the other half of the participants completed the unstructured blocks first followed by the structured blocks. Participants of both groups received neither explicit information on the midstream change in structure nor feedback on the correctness of each response throughout the task.

If the influence of the biased probabilities acquired over the structured blocks persisted throughout the task, the RT difference between the more probable and less probable triplets would be similar across the structured and unstructured blocks for participants completing the structured blocks first. Moreover, it could also be explored how long the influence of this already acquired knowledge would last. Meanwhile, prior knowledge of equal probabilities emerging over the unstructured blocks could also persist and influence the further acquisition of biased probabilities. Accordingly, for participants completing the unstructured blocks first, no RT difference between the triplets is expected over the unstructured blocks. The RT difference over the structured blocks would emerge only in a slower, more gradual manner (cf. Zhao et al., 2019). However, as the lack of RT difference could persist throughout the task, it is also conceivable that these participants would not acquire the biased probabilities over the structured blocks.

2. Material and methods

2.1. Participants

Fifty healthy young adults took part in the experiment.[2] They were undergraduate students from Budapest, Hungary. Participants had normal or corrected-to-normal vision, and according to the predefined

[2] Studies using the Alternating Serial Reaction Time (ASRT) task with effect size measures for the prior knowledge effect were not available. Therefore, when determining the sample size per group, we followed the guidelines set by some of the previous behavioral ASRT-studies (Hallgató, Győri-Dani, Pekár, Janacsek, & Nemeth, 2013; Horváth, Török, Pesthy, Nemeth, & Janacsek, 2019; Nemeth, Hallgato, Janacsek, Sandor, & Londe, 2009; Nemeth & Janacsek, 2011; Nemeth, Janacsek, & Fiser, 2013; Szegedi-Hallgató et al., 2017; Vékony et al., 2020). On average, the sample size in these studies was approximately 23 per group (SD = 10.6).

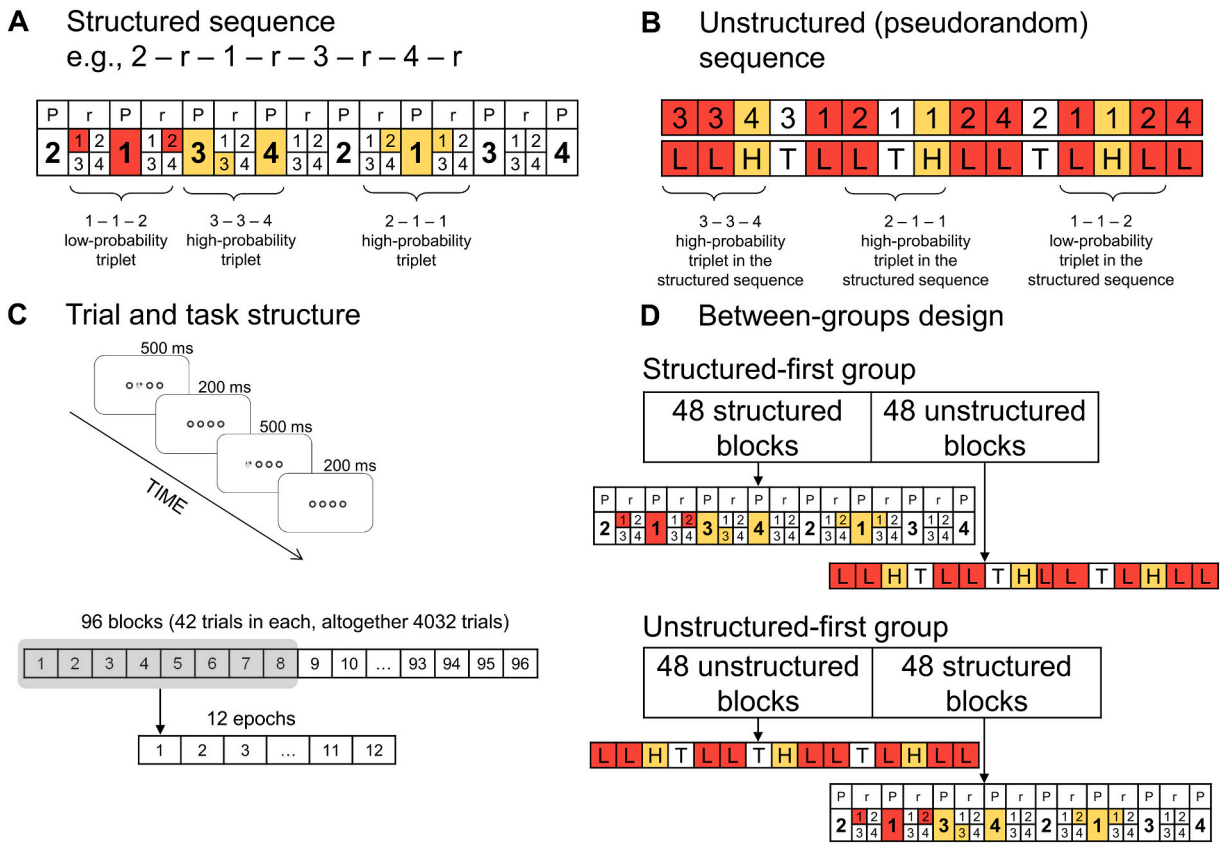

Fig. 1. Design of the experiment. (A) The presentation of stimuli in the structured sequence followed an eight-element regularity, within which pattern (P) and random (r) elements alternated with one another. Numbers denote the four different stimulus positions on the screen. The alternating regularity made some runs of three consecutive trials (triplets) more probable than others. High-probability triplets are denoted with gold shading and low-probability triplets are denoted with coral shading. (B) From the unstructured (pseudorandom) sequence, the alternating regularity was omitted, but the same unique triplets as in the structured sequence appeared with equal probability. Note that the probability of triplets only differs in the structured sequence and their probability is equal in the unstructured sequence. However, triplets in the unstructured sequence are still labeled as either high- or low-probability according to their actual probability in the structured sequence. Gold shading (upper row) and capital letter "H" (lower row) denote the third element of high-probability triplets, coral shading and "L" denote the third element of low-probability triplets, while white shading and "T" as "trill" denote the third element of some of those low-probability triplets that were eliminated from the analyses (see Statistical analysis section). Numbers denote the four different stimulus positions on the screen. Note that each stimulus (trial) is categorized as either the third element of a high- or a low-probability triplet in both sequences. For a given participant, at the level of unique triplets, the high- and low-probability triplets are the same in the structured and unstructured sequences. (C) In this version of the task, a stimulus appeared in one of four horizontally arranged empty circles on the screen in every 700 ms. Participants had to respond with one of the four response keys that corresponded to the position of the stimulus. They completed altogether 96 blocks, and eight-block-long units of the task were collapsed into larger time bins labeled as epochs. (D) While the Structured-first group (n = 25) completed 48 structured blocks followed by 48 unstructured blocks, the Unstructured-first group (n = 25) completed 48 unstructured blocks followed by 48 structured blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Descriptive data and performance on neuropsychological tests in the two groups.

	Structured-first group n = 25 $M(SD)$	Unstructured-first group n = 25 $M(SD)$	Between-groups Difference $t/U/\chi^2$
Gender [male/female]	8/17	8/17	1.00
Age [years]	21.5 (2.6)	20.8 (1.5)	274.50[a]
Education [years]	14.6 (2.1)	14.3 (1.6)	0.69
Handedness [LQ]	53.5 (49.3)	65.8 (28.7)	330.50[a]
Wisconsin Card Sorting Task [perseverative error percentage]	11.67 (3.81)	10.41 (2.02)	1.46[b]
Corsi blocks task [visuospatial short-term memory span; range: 3–9]	5.13 (0.54)	5.04 (0.68)	0.49
Counting span task [working memory span; range: 2–6]	3.80 (0.86)	4.08 (0.85)	−1.16
Go/No-Go task [discriminability index: hit rate minus false alarm rate]	0.72 (0.14)	0.71 (0.15)	0.40

Note. The two groups *did not differ* in any of the dependent variables and all participants performed in the normal range on the neuropsychological tests. Handedness was assessed with the Edinburgh Handedness Inventory revised version (Dragovic, 2004a, 2004b; Oldfield, 1971); LQ = Laterality Quotient, −100 means complete left-handedness, 100 means complete right-handedness.

[a] In the case of violating the assumption of normality, the Mann-Whitney U test was performed, and the U statistic is provided.

[b] In case of violating the assumption of homogeneity of variances, the robust Welch test of equality of means was performed, and the t statistic is provided.

inclusion criteria, none of them reported a history of any neurological and/or psychiatric condition, and none of them was taking any psychoactive medication. Half of the participants were randomly assigned to the Structured-first group ($n = 25$), while the other half was assigned to the Unstructured-first group ($n = 25$). The groups were differentiated by which half of the experimental task they started with; this is explained in the Procedure section below. Descriptive characteristics of participants in the two groups and their performance on standard neuropsychological tests are presented in Table 1. All participants provided written informed consent before enrollment and received payment (ca. 12 Euros) or course credit for taking part in the experiment. The study was approved by the United Ethical Review Committee for Research in Psychology (EPKEB) in Hungary and was conducted in accordance with the Declaration of Helsinki.

2.2. Experimental task

2.2.1. The Alternating Serial Reaction Time (ASRT) task

Implicit acquisition of second-order transitional probabilities was measured by a modified version of the ASRT task (Howard & Howard, 1997; Nemeth et al., 2010; Takács et al., 2018), which was optimized for a future fMRI study using a block design. In this task, a stimulus (a dog's head) appeared in one of four horizontally arranged empty circles on the screen (see Fig. 1C). Participants were instructed to press as quickly and accurately as possible one of the four response keys (Q, Y, M, or, O on a QWERTZ keyboard) that corresponded to the position of the stimulus (Q = leftmost position [left index finger], Y = second position from left to right [left thumb], M = third position from left to right [right thumb], O = rightmost position [right index finger]). In this task version, participants were clearly informed about the unusual mapping between spatial positions and response keys in the task instruction. During a practice phase with at least two mini-blocks of fifteen random trials each, participants had the chance to practice these stimulus-response mappings until they felt confident in proceeding to the main task. (The experimenters also required them to achieve 98% accuracy at least in the final mini-block).

In the ASRT task, unbeknownst to participants, the stimuli are presented according to an eight-element sequence, within which predetermined/pattern (P) and random (r) elements alternate with one another (Howard & Howard, 1997). For instance, 2 – r – 1 – r – 3 – r – 4 – r is one of the sequences, where numbers denote the four predetermined positions on the screen from left to right, and *r*s denote the randomly chosen positions out of the four possible ones (see Fig. 1A). There are 24 permutations of the four positions that could determine the applied sequence; however, because of the continuous presentation of the stimuli, there are only *six unique permutations*: 1 – r – 2 – r – 3 – r – 4 – r, 1 – r – 2 – r – 4 – r – 3 – r, 1 – r – 3 – r – 2 – r – 4 – r, 1 – r – 3 – r – 4 – r – 2 – r, 1 – r – 4 – r – 2 – r – 3 – r, and 1 – r – 4 – r – 3 – r – 2 – r (see also Figs. S1–S2). Note that each of these six permutations can start at any position; e.g., 1 – r – 3 – r – 4 – r – 2 – r and 2 – r – 1 – r – 3 – r – 4 – r are identical sequence permutations.

The alternating regularity yields a probability structure in which some chunks of three successive trials (triplets) occur more frequently than others. This characteristic of the task ensures that sensitivity to a biased distribution of triplets can be quantified. In the case of the 2 – r – 1 – r – 3 – r – 4 – r sequence, 2 – X – 1, 1 – X – 3, 3 – X – 4, and 4 – X – 2 triplets (X denotes the middle trial of the triplet) occur frequently since these triplets could have P – r – P or r – P – r structure. Meanwhile, for instance, 1 – X – 2 and 4 – X – 3 triplets occur less frequently since they could only have a r – P – r structure (see Fig. 1A). The former triplets are referred to as *high-probability* triplets, while the latter ones are referred to as *low-probability* triplets (e.g., Nemeth & Janacsek, 2011; Nemeth, Janacsek, Polner, & Kovacs, 2013). The construction of triplets could be considered as a method for identifying the hidden probability structure of the ASRT task. Namely, the final trial of a high-probability triplet is a probable (predictable) continuation for the first trial of the triplet, while the final trial of a low-probability triplet is a less probable continuation. For instance, in the case of the above-mentioned sequence, if the first trial of a triplet is position 3, it is more likely (with 62.5% probability) to be followed by position 4 as the third trial than either position 1, 2, or 3 (with 12.5% probability each). Each trial (stimulus) is categorized as either the third trial of a high- or a low-probability triplet. Accordingly, the construction of triplets is applied as a moving window throughout the entire stimulus set: The third trial of a triplet is also the second trial of the following triplet, and so on; thus, all stimuli are categorized this way (Kóbor et al., 2018; Kóbor, Janacsek, Takács, & Nemeth, 2017; Szegedi-Hallgató et al., 2017). There are 64 possible triplets in the task: 16 of them are high-probability triplets, and 48 are low-probability ones. With respect to the *unique* triplets, the third trials of high-probability triplets are five times more predictable based on the first trials than those of the low-probability triplets (see Figs. S1–S2).

2.2.2. Generation and selection of the unstructured sequences

Besides the *structured* ASRT sequences that included the alternating regularity, *unstructured* sequences were used, in which the alternating regularity was absent. The unstructured sequences had to meet two requirements. *First*, unstructured sequences had to contain the same 64 triplets as the structured sequences; however, the probability of occurrence of each unique triplet type had to be equal. Therefore, each of the 64 triplets had to occur 30 times in any of the unstructured sequences but without the presence and repetition of the alternating regularity (1920 triplets in total, see the second requirement). In this way, unstructured sequences could also be considered as pseudorandom sequences with the constraint that all triplets occurred with equal probability (25%). *Second*, unstructured sequences had to contain the same number of trials as structured sequences because they determined stimulus presentation in an equal number of blocks. This meant the presentation of altogether 1920 triplets distributed over 48 blocks with 40 triplets in each, respectively (see below). For this purpose, *without* the use of the alternating regularity, several trial sets were generated in MATLAB 2015a (The MathWorks Inc., Natick, 224 MA, USA). Particularly, by randomly changing one trial of the trial sets at a time, the trial set minimizing the deviation from the optimal 30 times of occurrence was selected (the maximal error was set to two). Using this algorithm, a dozen trial sets satisfying this criterion were kept.

These trial sets were then subjected to three further constraints: (1) the maximal repetition of a unique triplet in any of the blocks could be no more than four; (2) the maximal immediate repetition of a trial [position] could be no more than five across the entire trial set; (3) in larger time bins (16 blocks) of the unstructured trial set, the overall occurrence probability of triplets that can be categorized as high- vs. low-probability in the structured ASRT sequences should approximate 25% and 75%, respectively, since there are 16 unique high-probability and 48 unique low-probability triplets for a given ASRT sequence (see above the ASRT task description). This third constraint ensured that at the level of unique triplets, the transitional probabilities were equal. Six of the trial sets were appropriate regarding constraints (1) and (2). Stimuli of these six trial sets were categorized into *triplets* following either of the six unique structured ASRT sequences (see Fig. 1B); and, constraint (3), i.e., the ratio of the high- and low-probability triplets, was checked on these categorized trial sets. Finally, altogether 19 trial sets satisfied all three constraints and were kept using as *unstructured sequences*.

When assigning the structured ASRT and unstructured sequences to participants, we ensured that the distribution of the six unique ASRT sequence types was even across the two groups. The 1 – r – 2 – r – 3 – r – 4 – r sequence was used five times, and all the other sequences were used four times in each of the groups (i.e., for 25 participants per group). For each participant, the selection of a sequence from the six unique types was pseudorandom. The applied files containing the structured ASRT and unstructured sequences were matched one-to-one across the two groups. Note that for each respective participant, at the

level of unique triplets, the identified high- and low-probability triplets were the same in the unstructured sequences as in the structured ASRT sequences (see Fig. 1A–B). Indeed, the probability of triplets differed only in the structured sequences and their probability was equal in the unstructured sequences (see Figs. S1–S2). Meanwhile, in the remainder of the paper, triplets in the unstructured sequences are still referred to as either high- or low-probability according to their actual probability in the structured sequences.

As a result of the procedure used for generating, selecting, and matching the sequences, in the present sample, the distribution of high- and low-probability triplets did not differ across the four stimulus positions either in the structured ASRT ($\chi^2(3) = 4.86$, $p = .183$) or in the unstructured sequences ($\chi^2(3) = 0.02$, $p = .999$); in addition, these associations between triplet distribution and stimulus position did not differ across the sequence types (Wald $\chi^2(3) = 2.34$, $p = .504$). When the high- and low-probability triplet categories were collapsed, the distribution of stimulus positions across sequence types also did not differ ($\chi^2(3) = 1.56$, $p = .670$). In this way, lower-level characteristics of the sequences would not account for the assumed between-sequence RT variations related to acquiring the second-order transitional probability structure (cf. Reed & Johnson, 1994).

2.3. Procedure

An experimental trial started with the presentation of the stimulus at one of the four positions for 500 ms. After stimulus offset, the image of the four positions was displayed for 200 ms. Then, the next trial started, yielding a 700-ms-long inter-trial interval. The behavioral response (keypress) was expected during the whole trial from stimulus onset until the end of the trial (i.e., for altogether 700 ms, see Fig. 1C). These trial events were always the same with fixed durations, irrespective of whether participants provided correct, incorrect, or missing response(s). In this task version, no feedback was presented as a function of the quality of the response. The lack of feedback presentation and the fact that participants could proceed with the trial without providing the correct response ensured that each trial and each block had the same lengths, respectively. Importantly, only correctly responded trials were analyzed in the present study.

One block of the task contained 42 trials. There were 48 blocks with the structured ASRT sequence and 48 blocks with the unstructured sequence. In each of the structured blocks, the eight-element-long alternating regularity repeated five times after two starter trials that were not categorized as triplet elements (since also the foremost triplet technically required three successive trials). The alternating regularity was missing from the unstructured blocks, but, as in the structured blocks, 40 triplets followed the two starter trials that were not categorized as triplet elements. After each block, participants received feedback about their mean reaction time and accuracy in the given block. The length of this between-blocks "rest period" with feedback was jittered to be methodologically optimal for a future fMRI experiment (it lasted for 10, 12, or 14 s [mean = 12 s]). Altogether 96 blocks were completed (4032 trials in total).

The Structured-first group completed 48 structured blocks followed by 48 unstructured blocks. The Unstructured-first group completed 48 unstructured blocks followed by 48 structured blocks. All participants proceeded with the task from its structured/unstructured to unstructured/structured half without receiving information about any change in the task (see Fig. 1D). Two breaks (1.5 mins each) were inserted after the 32nd and 64th blocks, in which participants could have had a short rest. The experimental procedure lasted about 1.5 h including the administration of a short post-task questionnaire. This assessed participants' task-solving strategies and their consciously accessible knowledge about the structure of the task and the transitional probabilities (Kóbor et al., 2017; Nemeth, Janacsek, & Fiser, 2013; Song, Howard, & Howard, 2007). Namely, participants were asked whether (1) they followed any task-solving strategies to improve their performance, (2) if yes, to what extent they found it efficient; (3) whether they noticed anything special regarding the task; (4) whether they noticed any regularity in the sequence of stimuli; and (5) whether they noticed any substantial change in the sequence of stimuli. The first author (AK) qualitatively rated participants' answers to questions (1) and (2), and rated the answers to questions (3), (4), and (5) on a 5-item scale (1 = "Nothing noticed", 5 = "Total awareness"). None of the participants reliably reported noticing the alternating regularity, the presence and repetitions of the triplets, or any change in the stimulus sequence between the task halves (the mean score for the three questions was 1.006, $SD = 0.082$). Although participants reported several strategies they found somewhat facilitating (e.g., counting the stimuli, fixating to the center of the screen, catching the rhythm of trials by silently singing, bouncing their legs, or moving their fingers), these were unrelated to the hidden structure of the task. Only one participant reported trying to search for some "logic" in the sequence but as a subjectively inefficient strategy.

The current ASRT task version was written in and controlled by MATLAB 2015a using the Psychophysics Toolbox Version 3 (PTB-3) extensions (Brainard, 1997; Pelli, 1997). Stimuli were displayed on a 15″ LCD screen at a viewing distance of 100 cm. Neuropsychological tests (see Participants section) were administered a few days before the main experiment during a one-hour-long session.

2.4. Statistical analysis

Following the standard data analysis protocol established in previous studies using the ASRT task (e.g., Howard & Howard, 1997; Kóbor et al., 2017; Nemeth, Janacsek, Polner, & Kovacs, 2013; Song et al., 2007; Virag et al., 2015), two types of low-probability triplets – repetitions (e.g., 1 – 1 – 1, 4 – 4 – 4) and trills (e.g., 1 – 2 – 1, 2 – 4 – 2, see Fig. 1B) – were eliminated from the analyses because preexisting response tendencies have often been shown to them (Howard et al., 2004). In addition, eight-block-long units of the task were collapsed into larger time bins labeled as *epochs*, yielding altogether six structured epochs (containing the ASRT sequence) and six unstructured epochs (containing the unstructured sequence). From this point of view, while the Structured-first group performed six structured epochs followed by six unstructured epochs, the Unstructured-first group performed six unstructured epochs followed by six structured epochs. Epochs are labeled consecutively in this paper (1, 2, etc.) within each sequence type. For each participant and epoch, separately for high- and low-probability triplets, median RT was calculated only for correct responses.

Triplet learning on the RTs, i.e., faster RTs to high-probability than to low-probability triplets, was first quantified with a four-way mixed design analysis of variance (ANOVA) with Sequence (structured vs. unstructured), Triplet (high- vs. low-probability), and Epoch (1–6) as within-subjects factors and Group (Structured-first group vs. Unstructured-first group) as a between-subjects factor. Second, to more directly test the change in triplet learning as a function of the different sequence types, three-way mixed ANOVAs with Triplet and Epoch as within-subjects factors and Group as a between-subjects factor were performed on the RTs related separately to the structured and unstructured epochs. In all ANOVAs, the Greenhouse-Geisser epsilon (ε) correction (Greenhouse & Geisser, 1959) was used when necessary. Original *df* values and corrected (if applicable) p values are reported together with partial eta-squared (η_p^2) as the measure of effect size. LSD (Least Significant Difference) tests for pairwise comparisons were used to control for Type I error.

Regarding the possible experimental effects and their interpretation, the Triplet main effect implies *triplet learning* (faster RTs to high- than to low-probability triplets) and the Triplet * Epoch interaction implies *changes in triplet learning* as the task progresses, usually an increase across epochs (e.g., Janacsek, Ambrus, Paulus, Antal, & Nemeth, 2015; Kóbor et al., 2017; Nemeth et al., 2010; Nemeth, Janacsek, Polner, & Kovacs, 2013; Takács et al., 2017; Tóth et al., 2017). The Epoch main

effect implies *general skill (RT) improvements* reflecting more efficient visuomotor and motor-motor coordination due to practice (Hallgató et al., 2013; Juhasz, Nemeth, & Janacsek, 2019). The *prior knowledge effect* is indicated by the Sequence ∗ Triplet ∗ Group and/or the Sequence ∗ Triplet ∗ Epoch ∗ Group interactions: Namely, if prior knowledge of the transitional probabilities influences later stimulus processing, triplet learning per se or its change over time should differ between structured and unstructured epochs *and* across the two groups experiencing the structured and unstructured epochs in the opposite order. In the Results section below, we use these terms when describing the observed statistical effects.

To follow up the prior knowledge effect, triplet learning scores in the structured and unstructured epochs were calculated as the RT difference between the triplet types (RTs to low-probability triplets minus RTs to high-probability triplets). *Overall triplet learning scores* were considered for the structured and unstructured epochs, respectively, as the mean of the scores calculated for each of the six epochs. The overall triplet learning scores for the structured and unstructured epochs were first compared within each group. Then, these scores were compared between the groups. Finally, the change in mean RTs across the structured and unstructured epochs separately for the high- and low-probability triplets was compared within each group.

To test the *persistence* of the prior knowledge effect, triplet learning scores were further analyzed in the Structured-first group. To find a balance between increased power and capturing the time course of persistence, triplet learning scores were averaged over *two consecutive epochs* (i.e., "thirds") of the structured and unstructured sequences, respectively. Then, these scores were compared against zero in each sequence type. Finally, these scores were compared between the corresponding thirds of the structured and unstructured sequences.

3. Results

3.1. Overall analysis

The Sequence (structured vs. unstructured) by Triplet (high- vs. low-probability) by Epoch (1–6) by Group (Structured-first group vs. Unstructured-first group) *overall* ANOVA on the RTs revealed the significant main effects of Sequence, $F(1, 48) = 6.77$, $p = .012$, $\eta_p^2 = .124$, Triplet, $F(1, 48) = 45.90$, $p < .001$, $\eta_p^2 = .489$, and Epoch, $F(5, 240) = 35.91$, $\varepsilon = .612$, $p < .001$, $\eta_p^2 = .428$. As these main effects were qualified by significant higher-order interactions, only the latter effects are detailed below.

3.1.1. Triplet learning

The Sequence ∗ Triplet, $F(1, 48) = 22.92$, $p < .001$, $\eta_p^2 = .323$, and the Triplet ∗ Epoch, $F(5, 240) = 2.42$, $p = .036$, $\eta_p^2 = .048$, interactions were significant, while the Sequence ∗ Triplet ∗ Epoch, $F(5, 240) = 2.18$, $\varepsilon = .814$, $p = .072$, $\eta_p^2 = .043$, interaction was a trend level. These effects indicated that the change in triplet learning over the course of the task differed between the structured and unstructured epochs.

3.1.2. General skill improvements

The significant Sequence ∗ Group, $F(1, 48) = 69.87$, $p < .001$, $\eta_p^2 = .593$, and the Sequence ∗ Epoch ∗ Group, $F(5, 240) = 33.59$, $\varepsilon = .706$, $p < .001$, $\eta_p^2 = .412$, interactions showed that between-groups differences emerged as a function of first experiencing the structured or the unstructured half (i.e., six epochs) of the task. Particularly, while the Structured-first group became increasingly faster over the structured epochs due to practice and showed similar RTs over the unstructured epochs, this was reversed in the Unstructured-first group, where increasingly faster RTs were observed over the unstructured epochs and similar RTs over the structured epochs (see Fig. 2). This effect suggests that general skill improvements were found in the first half of the task, irrespective of whether this half was structured or unstructured and the distribution of triplets. Relatedly, the following *nonsignificant* main effects and interactions emerged: main effect of Group, $F(1, 48) = 1.96$, $p = .168$, $\eta_p^2 = .039$, Epoch ∗ Group interaction, $F(5, 240) = 0.47$, $\varepsilon = .612$, $p = .706$, $\eta_p^2 = .010$, and Sequence ∗ Epoch interaction, $F(5, 240) = 1.20$, $\varepsilon = .706$, $p = .313$, $\eta_p^2 = .024$.

3.1.3. Prior knowledge effect

The significant Triplet ∗ Group interaction, $F(1, 48) = 4.92$, $p = .031$, $\eta_p^2 = .093$, was qualified by the significant Sequence ∗ Triplet ∗ Group interaction, $F(1, 48) = 7.96$, $p = .007$, $\eta_p^2 = .142$. Importantly, the latter indicated that the difference in triplet learning between the structured and unstructured epochs varied across the groups, which is regarded as the prior knowledge effect (see Fig. 2). This effect did not reliably vary as a function of practice with the task, as shown by the nonsignificant Sequence ∗ Triplet ∗ Epoch ∗ Group interaction, $F(5, 240) = 0.61$, $\varepsilon = .814$, $p = .661$, $\eta_p^2 = .012$. Relatedly, the modulating effect of structured vs. unstructured epochs on triplet learning was also supported by the significant Triplet ∗ Epoch ∗ Group interaction, $F(5, 240) = 2.31$, $p = .045$, $\eta_p^2 = .046$, showing that if both task halves with structured and unstructured epochs were collapsed, the trajectory of triplet learning would differ across the groups.

3.2. Follow-up of the prior knowledge effect

To follow up the prior knowledge effect, pairwise comparisons contrasting the overall triplet learning scores were performed (see Fig. 3). In the Structured-first group, the triplet learning score was similar between the structured and unstructured epochs (6.3 ms vs. 4.6 ms, $p = .171$). Thus, the behavioral effect of biased triplet probabilities (i.e., high- and low-probability triplets in the structured epochs) persisted even after this bias was eliminated (i.e., the unique triplets occurred with equal probability in the unstructured epochs). Meanwhile, in the Unstructured-first group, the triplet learning score was significantly higher over the structured epochs than over the unstructured epochs; in the latter, it was virtually zero (5.9 ms vs. −0.4 ms, $p < .001$). In addition, the triplet learning score did not differ between the groups over the structured epochs (6.3 ms vs. 5.9 ms, $p = .840$), but it was significantly higher in the Structured-first group than in the Unstructured-first group over the unstructured epochs (4.6 ms vs. −0.4 ms, $p < .001$).

In the Structured-first group, mean RTs on the high- and low-probability triplets decreased from the structured to the unstructured epochs to a similar extent (high-probability triplets: 392 ms to 383 ms [Diff = 9 ms], $p = .003$; low-probability triplets: 399 ms to 388 ms [Diff = 11 ms], $p < .001$; the difference in RT decrease between high- and low-probability triplets was not significant, $p = .226$), indicating only general skill improvements from the structured to the unstructured epochs. In contrast, in the Unstructured-first group, a larger RT decrease was found on the high-probability triplets (388 ms to 366 ms [Diff = 22 ms], $p < .001$) than on the low-probability ones (388 ms to 372 ms [Diff = 16 ms], $p < .001$; the difference in RT decrease between high- and low-probability triplets was significant, $p < .001$) from the unstructured to the structured epochs, indicating triplet learning over the structured epochs.

3.3. Persistence of the prior knowledge effect

To test the persistence of the prior knowledge effect in the Structured-first group, triplet learning scores were averaged over $epoch_1$ and $epoch_2$ (M_{e1e2}), $epoch_3$ and $epoch_4$ (M_{e3e4}), $epoch_5$ and $epoch_6$ (M_{e5e6}), respectively. These new scores were compared against zero and between the structured and unstructured sequences. The obtained results are presented in Fig. 4A and detailed below.

The extent of triplet knowledge differed significantly from zero over

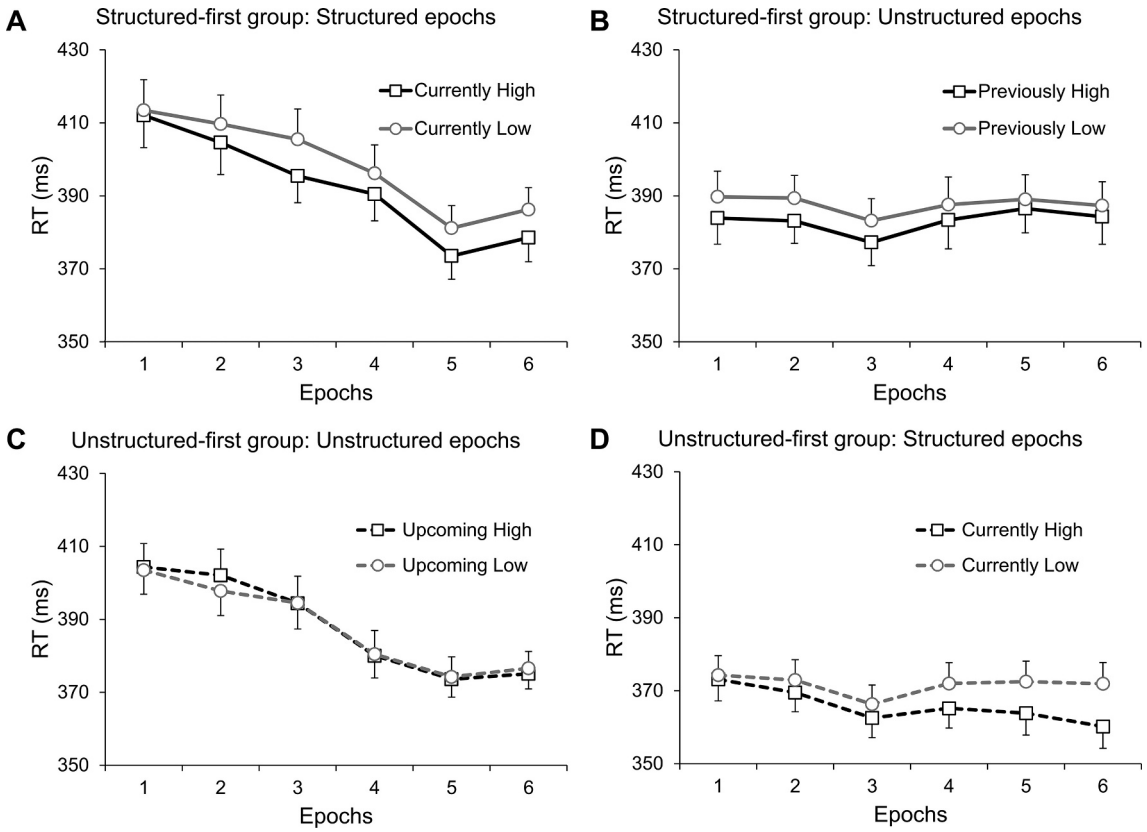

Fig. 2. Temporal dynamics of triplet learning across groups and sequence types. Group-average RTs (A–B: Structured-first group; C–D: Unstructured-first group) for correct responses as a function of time bin (epochs 1–6) and triplet type (currently/previously/upcoming high- vs. low-probability triplets, according to their actual probability in the given sequence and the order of the sequence in the given group) are presented in the structured (A, D) and unstructured (B, C) epochs. Error bars denote standard error of mean.

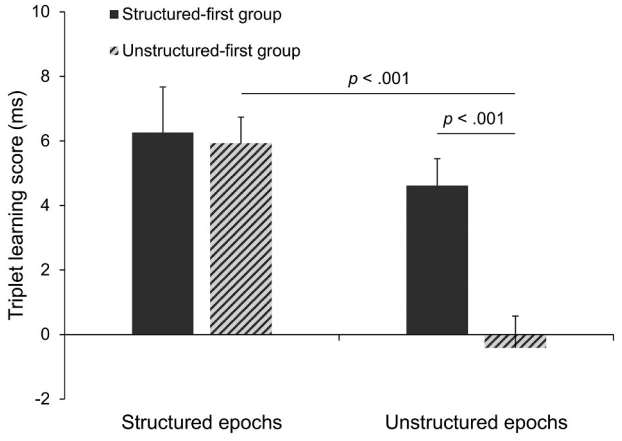

Fig. 3. Persistence of the acquired implicit knowledge. Group-average overall (mean) triplet learning scores (RTs to low- minus RTs to high-probability triplets) are presented in the Structured-first and Unstructured-first groups for the structured and unstructured epochs, respectively. Error bars denote standard error of mean.

all thirds of the structured and unstructured sequences (all *t*s ≥ 2.11, *p*s ≤ .045), except for the very first one at the beginning of the task ($t(24) = 1.26$, $p = .221$). This indicated the presence of triplet knowledge from the second third of the structured sequence throughout the task. Triplet knowledge did not differ between the unstructured and structured sequences during the first (M_{e1e2}: 6.0 ms vs. 3.2 ms, respectively, $t(24) = -0.96$, $p = .349$) and second thirds of the task (M_{e3e4}: 5.1 ms vs. 7.9 ms, respectively, $t(24) = 1.35$, $p = .190$). In contrast, triplet knowledge over the last third of the unstructured sequence was significantly lower than over the last third of the structured sequence (M_{e5e6}: 2.8 ms vs. 7.7 ms, respectively, $t(24) = 2.46$, $p = .022$). The decreasing extent of triplet knowledge is also noticeable in Fig. 2B as RTs to high- and low-probability triplets approaching one another in the last third of the unstructured sequence. These results altogether suggest that participants acquired the triplet knowledge in the second third of the structured sequence; and, after biased probabilities had been removed from the stimulus stream, the update of the triplet knowledge was evident in behavior only in the final third of the unstructured sequence.

3.4. Separate analysis of the structured and unstructured epochs

The Triplet by Epoch by Group ANOVA on the RTs related to the *structured* epochs revealed the significant main effects of Triplet, $F(1, 48) = 56.00$, $p < .001$, $\eta_p^2 = .538$, Epoch, $F(5, 240) = 27.54$, $\varepsilon = .700$, $p < .001$, $\eta_p^2 = .365$, and Group, $F(1, 48) = 9.25$, $p = .004$, $\eta_p^2 = .162$. These effects were qualified by the significant Triplet * Epoch, $F(5, 240) = 4.55$, $p = .001$, $\eta_p^2 = .087$, and Epoch * Group, $F(5, 240) = 15.77$, $\varepsilon = .700$, $p < .001$, $\eta_p^2 = .247$, interactions, indicating that triplet learning increased with practice and general skill improvements differed between the groups (see Fig. 2A, D). Triplet learning and its change over the structured epochs did not differ between the groups, as shown by the nonsignificant Triplet * Group, $F(1, 48) = 0.04$, $p = .840$, $\eta_p^2 = .001$, and Triplet * Epoch * Group interactions, $F(5, 240) = 1.54$, $p = .177$, $\eta_p^2 = .031$.

The same Triplet by Epoch by Group ANOVA on the RTs related to the *unstructured* epochs revealed the significant main effects of Triplet, $F(1, 48) = 10.61$, $p = .002$, $\eta_p^2 = .181$, and Epoch, $F(5, 240) = 13.45$,

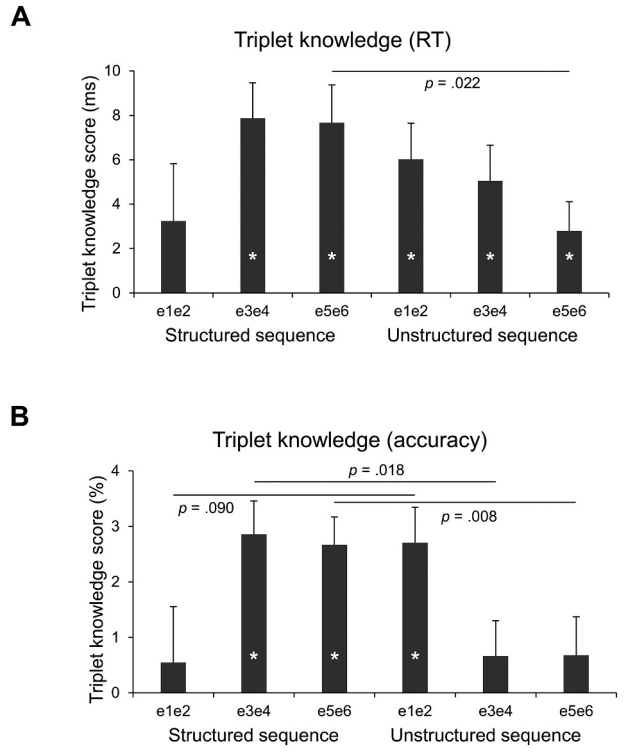

Fig. 4. Temporal characteristics of persistency. In the Structured-first group, group-average triplet knowledge scores measured by RTs (A) and accuracy (B) averaged over two consecutive epochs (i.e., "thirds") of the structured and unstructured sequences, respectively, are presented. Error bars denote standard error of mean. White asterisks denote that the given score significantly differs from zero ($p < .050$).

$\varepsilon = .605$, $p < .001$, $\eta_p^2 = .219$, while the Triplet ∗ Epoch interaction was not significant, $F(5, 240) = 0.24$, $p = .945$, $\eta_p^2 = .005$. Importantly, the significant Triplet ∗ Group interaction, $F(1, 48) = 15.23$, $p < .001$, $\eta_p^2 = .241$, showed that triplet learning was larger in the Structured-first group than in the Unstructured-first group (4.6 ms vs. -0.4 ms) over the unstructured epochs, but this did not change with time (nonsignificant Triplet ∗ Epoch ∗ Group interaction, $F(5, 240) = 1.33$, $p = .251$, $\eta_p^2 = .027$). The trajectory of general skill improvements differed between the groups (significant Epoch ∗ Group interaction, $F(5, 240) = 16.12$, $\varepsilon = .605$, $p < .001$, $\eta_p^2 = .251$, see Fig. 2B, C), and the groups did not differ in overall RT (nonsignificant Group main effect, $F(1, 48) = 0.09$, $p = .764$, $\eta_p^2 = .002$) over the unstructured epochs.

3.5. Analysis of accuracy

Since only the RTs of the correctly responded trials were analyzed, it should be ensured that the two groups did not differ in accuracy. Therefore, the Sequence by Triplet by Epoch by Group ANOVA was also conducted on accuracy data (calculated as the ratio of correct responses for each participant and epoch, separately for high- and low-probability triplets). As indicated by the nonsignificant main effect of Group, $F(1, 48) = 1.53$, $p = .221$, $\eta_p^2 = .031$, the two groups were comparable in overall accuracy (Structured-first group: 86.4%; Unstructured-first group: 88.1%).

Although the analysis of accuracy is not the focus of this study, for the sake of completeness, we provide the other significant main effects and interactions revealed in this ANOVA, but these are not detailed. The main effects of Triplet, $F(1, 48) = 25.25$, $p < .001$, $\eta_p^2 = .345$, and Epoch, $F(5, 240) = 7.42$, $\varepsilon = .639$, $p < .001$, $\eta_p^2 = .134$, were significant. Relatedly, the Sequence ∗ Triplet, $F(1, 48) = 4.91$, $p = .032$, $\eta_p^2 = .093$, and the Sequence ∗ Triplet ∗ Epoch, $F(5, 240) = 3.49$, $p = .005$, $\eta_p^2 = .068$, interactions were also significant. In brief, responses to high-probability triplets were more accurate than those to low-probability ones. However, while this difference in accuracy increased over the structured epochs, it gradually decreased over the unstructured epochs.

The Sequence ∗ Group, $F(1, 48) = 9.75$, $p = .003$, $\eta_p^2 = .169$, and the Sequence ∗ Epoch ∗ Group, $F(5, 240) = 7.44$, $\varepsilon = .524$, $p < .001$, $\eta_p^2 = .134$, interactions were significant, as well. The Sequence ∗ Triplet ∗ Epoch ∗ Group interaction was a trend level, $F(5, 240) = 1.92$, $p = .091$, $\eta_p^2 = .039$. The latter effect indicated that the above-described Sequence ∗ Triplet ∗ Epoch interaction was mostly driven by the responding pattern of the Structured-first group. Particularly, in the Structured-first group, while the difference in accuracy between high- and low-probability triplets increased over the structured epochs, it tended to decrease over the unstructured epochs. In the Unstructured-first group, accuracy between high- and low-probability triplets differed only over the structured epochs.

The results of comparing triplet knowledge measured by accuracy calculated for each third of each sequence in the Structured-first group were in line with these effects (see Fig. 4B). The extent of triplet knowledge differed significantly from zero over the middle and last thirds of the structured sequence and over the first third of the unstructured sequence (all $ts \geq 4.24$, $ps < .001$). Accordingly, triplet knowledge tended to be higher over the first third of the unstructured sequence than over the first third of the structured sequence (M_{e1e2}: 2.7% vs. 0.6%, respectively, $t(24) = -1.77$, $p = .090$). In contrast, triplet knowledge was significantly lower over the last two thirds of the unstructured sequence than over the corresponding thirds of the structured sequence (M_{e3e4}: 0.7% vs. 2.9%, respectively, $t(24) = 2.55$, $p = .018$; M_{e5e6}: 0.7% vs. 2.7%, respectively, $t(24) = 2.91$, $p = .008$). These results suggest that updating the triplet knowledge after biased probabilities had been removed was as fast as acquiring that knowledge in the first place.

4. Discussion

4.1. Summary of results

This study investigated whether the implicitly acquired knowledge of a second-order transitional probability structure influenced the processing of unpredictable transitional probabilities across phases of a learning task. To this end, the changes in RTs to more probable and less probable short-range transitional probabilities (triplets) embedded in a stimulus sequence were tracked. The stimulus sequence changed over the experimental task because biased triplet probabilities were present in one-half of the task blocks and absent in the other half, without explicitly denoting this change at the surface level.

In line with our assumptions, while the participant group completing the structured half of the task first showed triplet learning across both the structured and unstructured blocks, the participant group completing the unstructured half first showed triplet learning only over the structured blocks and not over the unstructured blocks. Based on the performance of the group completing the structured half of the task first, it seems that the already acquired implicit knowledge of the short-range transitional probabilities persisted across the learning phases, even after the bias in the transitional probabilities had been removed. This persistence characterized two-thirds of the unstructured blocks. Then, the update of prior knowledge became evident in RT triplet learning over the last third of these blocks. The results also imply that the updating process took longer than the primary acquisition, which required only one-third of the structured blocks. Based on the performance of the group completing the unstructured half of the task first, it seems that the protracted exposure to unbiased transitional probabilities did not negatively influence the acquisition of the biased transitional probabilities later in the task. Therefore, any potential

expectation or knowledge built upon the pseudorandom stimuli was also updated to promote the acquisition of the newly experienced biased transitional probabilities.

4.2. Persistent implicit statistical knowledge

Participants completing the structured blocks first similarly perceived the relations of stimuli in both types of blocks. That is, their perception could have been influenced by the primarily experienced transitional probability structure. In other words, because of the task environment, they might have worked up a tendency towards pattern detection, which could have resulted in forming implicit expectations about the upcoming stimuli. Then, these expectations remained persistent throughout the task.

To explain the observed persistency, one should consider the characteristics of the given learning environment. In the present task, acquisition happened in an incidental and implicit manner: our participants did not know that they were in a learning situation, they did not have information on whether the sequence of stimuli was random or followed any underlying pattern, the critical change point between the task halves remained unnoticed, and they were not required to actively or explicitly predict the probability of the next stimulus. In addition, they did not receive feedback (or any reward) on the correctness of their responses. Meanwhile, participants were instructed to maintain a certain level of speed and accuracy, but, for them, this was the only explicit goal of the task. They successfully achieved this goal, as shown by the behavioral results indicating general skill improvements due to practice. This performance improvement was mostly independent of the change in the underlying probability structure. Therefore, it seems that as participants had gained confidence in task solving, they followed their already established, automatized strategy on stimulus processing and responding (cf. Karuza et al., 2016). As the surface of the task remained consistent, they had no reason to doubt their current implicit beliefs about the probability of the upcoming stimulus (cf. Zinszer & Weiss, 2013). This might have promoted the persistently faster processing of the stimuli that occurred with high probability only in the previous task half.

From a broader perspective, it could be adaptive that the acquired representations of the structured stimuli remain persistent over time and robust to change. This way, the representations could remain sensitive to the primary transitional probability structure later in time, although other structures are simultaneously acquired (cf. Gebhart et al., 2009; Qian et al., 2012; Todd et al., 2011; Todd et al., 2020). This might be even more pronounced if no explicit cue or performance deterioration signals the need for an updating process. Supporting this notion, during the acquisition of two different statistical structures, a tendency towards neural efficiency coupled with diminished sampling of the input underlying the second statistical structure has been shown (Karuza et al., 2016). Accordingly, we assume that such a "processing efficiency" might explain our results on the transition from structured to pseudorandom stimuli.

4.3. Temporal characteristics of persistency

It has already been demonstrated that the primarily acquired implicit knowledge of the biased distribution of transitional probabilities remains stable over longer time periods, such as one week (Nemeth & Janacsek, 2011) or even one year (Romano, Howard, & Howard, 2010). Moreover, this knowledge is resistant to short periods of interfering sequences (that partially overlap with the primarily practiced sequence) not only after 24 h but also after one year (Kóbor et al., 2017). The present study could extend these results on persistency as follows. If there is an essential change in the stimulus probabilities characterizing the given environment, the duration required for updating the existing probabilistic representations seems to be longer than the duration required for acquiring these representations, at least at the behavioral level.

In detail, for participants completing the structured blocks first, acquiring the biased probability structure required one-third of the structured sequence; then, this knowledge remained persistent until the end of the task. However, participants were also sensitive to the lack of bias or the altered probability of the unique triplets over the unstructured sequence. Particularly, while triplet knowledge measured by RTs was comparable over the first two-thirds of the structured vs. unstructured sequences, triplet knowledge was decreased in the last third of the unstructured sequence as compared with the structured sequence. Thus, participants needed to complete two-thirds of the unstructured sequence to update their existing knowledge of the probability structure, which was acquired after the completion of only one-third of the structured sequence. When triplet knowledge was defined by differences in accuracy, updating was more pronounced and became evident earlier: Triplet knowledge was lower over the middle and last thirds of unstructured sequence than that of the structured sequence. Indeed, after one-third of the task blocks, triplet knowledge abruptly increased when the bias was present and dropped when the bias was eliminated. Overall, the results of participants completing the structured blocks first might indicate an "implicit need" for updating the prior representations of the probability structure. At the same time, these results also highlight the constraining effect of the primarily acquired, possibly overlearned statistical structure in the adaptation to a new environment (cf. Bulgarelli & Weiss, 2016; Gebhart et al., 2009).

It has been suggested that successful adaptation to a range of similar tasks requires the forgetting or weakening of some specific features of the already acquired representations (Robertson, 2018). As described above, in the present case, this would have been the forgetting of the initial triplet probability information when starting the other task half. It is plausible to assume that after having had performed even more unstructured blocks, participants would have learned that the previously high-probability triplets no longer occurred with higher probability than the previously low-probability ones, and, therefore, the initial triplet probability information would have been forgotten or "unlearned". However, in accordance with the findings of Szegedi-Hallgató et al. (2017) indicating the coexistence of the previously and the recently acquired implicit knowledge of the changed statistical structure in the ASRT task, it is more likely that, at the level of triplet representations, no "extinction" or "unlearning" happened. Evidence from human and animal studies suggests that adaptation to different contexts does not involve the complete removal of representations of the previous context (Bulgarelli & Weiss, 2016; Gordon, Bilolikar, Hodhod, & Thomas, 2020; Qian et al., 2012). Instead, the formation of new representations, the reconsolidation or inhibition of the previously created ones, and the switching between multiple representations seem more likely (Chandler & Gass, 2013). Either of the latter processes supports the interpretation that in the present experiment, stimulus processing was determined by prior representations of the transitional probability structure that changed slowly with accumulating experiences about the ongoing stimulus context (cf. Daw et al., 2011; Griffiths et al., 2008; Shohamy & Daw, 2015). The exact mechanisms by which this slow change might have occurred has yet to be determined, and formal models should be developed to investigate the temporal dynamics of these mechanisms (cf. R. Frost et al., 2019; Karuza et al., 2016; Qian et al., 2012; Zhao et al., 2019).

4.4. Exposure to pseudorandom stimuli

Over the structured blocks, participants completing the unstructured blocks first showed a triplet learning trajectory comparable to that of the other group (nonsignificant Triplet * Group and Triplet * Epoch * Group interactions, see also Fig. 2A, D). With an unsignaled change in the probability structure, the pervasive experience with pseudorandom stimuli could have also caused an entrenchment effect. In this case, these participants could have started the acquisition

of the biased probability structure with some disadvantage or could have showed the complete lack of triplet learning when exposed to the structured blocks. Instead, according to the results, it seems that prior experience with equal transitional probabilities did not negatively influence the further acquisition of the biased probability structure.

As an explanation for the triplet learning performance of these participants, it is conceivable that they might have primarily established a wider hypothesis space about the properties of the stimuli, since they could not extract complex transitional probabilities over the unstructured blocks. Such representations could be useful if the stimuli considered as random in the given environment with limited observations in fact followed some structure. With a wider hypothesis space, stimulus processing and acquisition might have proceeded flexibly, enabling the acquisition of the statistical structure when it was indeed present. In support of this idea, similar results were found in a binary choice task testing probability-matching behavior (i.e., matching choice probabilities to outcome probabilities instead of the optimal maximizing strategy). In that task, the transition between the no pattern (no serial dependence in the sequence) and pattern half (repeating deterministic sequence) was clearly indicated. Results showed that participants who were more prone to search for patterns in the no pattern half of the task showed higher accuracy in the pattern half as compared with those participants who were less prone to follow any complex search strategy (Gaissmaier & Schooler, 2008).

4.5. Perception and acquisition of changing statistical structures

Earlier studies using different paradigms showed mixed results on how individuals updated their already acquired knowledge of the underlying probabilities when these probabilities changed. It was found previously that individuals accurately estimated the hidden probability parameter of a nonstationary stochastic environment as well as quickly updated their estimates (Gallistel, Krishan, Liu, Miller, & Latham, 2014). In this task, participants assessed the proportion of one stimulus category and had the opportunity to update their estimates on a trial-by-trial basis. Importantly, at the beginning of the task, they were told that probabilities could unexpectedly change. Similarly, in another experiment where subsequent numerical values had to be predicted, participants updated each prediction as a function of their explicitly denoted prediction errors. By tracking the prediction errors, after an unsignaled change in the distribution of the values during the task, participants could adjust their predictions (Nassar, Wilson, Heasly, & Gold, 2010). The quick adaptation to changing probabilities was also observed when choosing between two options associated with different probabilities and reward magnitudes, i.e., with clear feedback signals (Behrens, Woolrich, Walton, & Rushworth, 2007).

These studies altogether suggest that effective decision making necessitates the continuous tracking of the environmental probabilities and the evaluation of each signal that possibly implies a change in these probabilities. However, these observations have been derived from situations in which active agents were required to make explicit decisions that pertained directly to the probabilistic features of the ongoing task modeling volatile environments. The latter characteristics possibly explain why the present results contrast with earlier findings. The ASRT task used in this study should not be considered as a(n) (explicit) decision-making or probabilistic reinforcement-learning paradigm in which quick updating of beliefs could happen (Bulgarelli & Weiss, 2016). Instead, the type of learning that this task measures more likely fits into the category of unsupervised statistical learning (Fiser & Aslin, 2001). It intends to model a stable stimulus environment with low volatility where hidden probabilistic regularities occur interspersed with noise in the form of nonadjacent transitional probabilities. These features could contribute to the persistence of the acquired regularities rather than to the abrupt change of the related representations.

A paradigm more similar to the ASRT task is the classical serial reaction time (SRT) task (e.g., Nissen & Bullemer, 1987), where a repeating deterministic sequence guides stimulus presentation in the structured blocks. In the SRT, performance usually deteriorates on the unstructured blocks with random or pseudorandom stimuli, meaning that RTs suddenly increase compared to the level reached by the end of the last structured block. Meanwhile, in the present study, participants completing the structured blocks first showed persistent triplet learning performance over several blocks of pseudorandom stimuli in terms of RTs. It is possible that in the case of probabilistic sequences (used in the ASRT task) as opposed to deterministic ones, the acquisition processes are more sensitive to smooth transitions between stimuli or chunks of stimuli. This specific sensitivity evolved in participants practicing the structured blocks first might have led the extraction of triplets even over the unstructured blocks of the task (see also the Transfer of prior knowledge section). In addition, as opposed to deterministic and pseudorandom sequences, the probabilistic sequence might have provided learnable but sufficiently novel information on a trial-by-trial basis (Maheu, Meyniel, & Dehaene, 2020), promoting the relatively fast acquisition of the statistical structure as well as its persistence.

Other studies using linguistic stimuli with transitional probabilities have started to investigate how to attenuate the persistent effect of the already acquired statistical representations (Weiss, Schwob, & Lebkuecher, 2019). By presenting two artificial speech streams in smaller alternating blocks, individuals were able to learn both statistical structures underlying the input streams, without using explicit contextual cues (e.g., change in speaker) denoting the transitions across streams (Zinszer & Weiss, 2013). However, if statistically incongruent, interfering statistical structures determined the stimuli, the formation of multiple representations was limited (Weiss et al., 2009). Importantly, if individuals were exposed to the second statistical structure immediately after learning had occurred on the first structure presented for a restricted time, both structures were learned. In addition, the different contextual cues did not further enhance performance (Bulgarelli & Weiss, 2016). Altogether, it seems that overlearning the first statistical structure and low variability in how the statistical structures are presented could decrease the attention paid to the input stream, thereby deteriorating the acquisition of the new structure (Bulgarelli & Weiss, 2016). This explanation might be feasible in the case of our findings; however, it should be noted that these studies tested the transition(s) between different statistical structures in the linguistic domain, while our study investigated the unsignaled transition from the presence to the absence of a structure in the visuomotor domain. Furthermore, the second-order nonadjacent transitional probabilities applied in the present task differed in structure and complexity from those transitional probabilities applied earlier. Nevertheless, we can contribute to this research field by confirming the presence of the primacy effect in a unique multi-context unsupervised learning environment and, this way, by extending the validity of this effect to unlearnable pseudorandom stimuli.

4.6. Transfer of prior knowledge

Considering the underlying processes, the present findings raise the question of whether learning transfer has occurred across the task halves. Studies testing the transfer (generalization) of perceptual and motor knowledge usually compare performance observed during a training task with performance observed during a similar testing condition, such as in a familiar task with new parameters or in a related but novel task. Successful transfer occurs if the experience gathered on the training task appears as a performance gain on the novel task (e.g., Dorfberger, Adi-Japha, & Karni, 2012; Karni, 1996; Karni & Bertini, 1997; Korman, Raz, Flash, & Karni, 2003).

In the statistical-sequence learning literature, the implicit transfer of both the perceptual and the motor sequence was shown in a version of the ASRT task that, in the testing phase, included a novel, previously unpracticed alternating motor or perceptual sequence with the same type of stimuli (Hallgató et al., 2013; Nemeth et al., 2009). In a

deterministic SRT task, the second-order transitional probability structure was implicitly transferred from the training to the testing phase, where the perceptual features of the stimuli differed (i.e., first-order structure: locations arranged horizontally or according to a square, Huang et al., 2017). Likewise, experiments using the artificial grammar learning task found the implicit transfer of sequential dependencies to novel vocabularies (Tunney & Altmann, 2001). Relatedly, unconscious within- and between-modalities transfer of artificial grammars was shown between training and test strings that changed at the surface level (letters in different vocabularies, notes, symbols) but remained structurally the same (Scott & Dienes, 2010). Another line of research found learning transfer in both directions between different types of memory tasks (motor skill task and word list task) via the extraction of high-level relations between the elements (Mosha & Robertson, 2016).

In contrast to these studies, the present experiment followed a different design: The surface of the stimuli remained the same across the two task phases, but their overall underlying structure changed. In this sense, the observed effect might not be considered as a classical perceptual-motor transfer effect. Indeed, it more likely captures a cognitive transfer effect: After a short experience with the unstructured sequence, participants completing the structured blocks first might have implicitly identified the features common (i.e., triplets) across the two task halves, which might have supported the generalization of the acquired transitional probability structure (cf., Qian et al., 2012; Robertson, 2018; Winkler & Cowan, 2005). Thus, the triplets as the critical building blocks of the structure might have been implicitly recalled in a later phase of task solving, even if their frequencies had changed. On the contrary, participants completing the unstructured blocks first only perceived the relations of stimuli primarily as triplets when they completed the ASRT sequence with biased probabilities. This would be in line with our recent findings that sensitivity to multiple regularities in the ASRT task seems to be grounded in the implicit extraction of the triplet-level probability structure (e.g., Kóbor et al., 2019; Szegedi-Hallgató, Janacsek, & Nemeth, 2019). Together with the previously described various transfer effects, the implicitly acquired prior knowledge seems to be robust to changes in both the surface and the underlying structure of the stimuli.

Related to the present task, an alternative experimental design with biased triplet probabilities would unequivocally test the transfer of the acquired implicit knowledge. For instance, one might use the ASRT sequence as the “structured sequence” and create another “less structured” sequence by keeping the biased distribution of high- (62.5%) and low-probability (37.5%) triplets but omitting the alternating regularity. In a similar between-subjects design, by presenting either the structured or the less structured sequence in the first half of the task and the other sequence in the second half, a future study might compare triplet learning between these two sequences. To follow previous experiments testing the transfer effect, the stimuli in the second half of the task might be different at the surface level (e.g., arrows or colors instead of horizontally arranged positions), but this is not necessary (cf. Gebhart et al., 2009). In another version of this experiment, the less structured sequence could be presented in both task halves for one of the groups, while the structured sequence followed by the less structured sequence could be presented for the other group. In this version, stimuli should differ at the surface level in the second half of the task.

If triplet learning occurs in both sequences, but only after participants completed the structured sequence first followed by the less structured one, it will indicate that knowledge of the transitional probability structure has been transferred across the task halves. However, for participants completing the less structured sequence first or completing only less structured sequences in both halves, we assume that a modest degree of triplet learning would also occur on these less structured sequences because of the initial sensitivity to the triplet-level probability structure (see above). This needs to be tested in additional experiments.

4.7. Methodological considerations

From a methodological point of view, it is not obvious how one investigates what has been learned about the statistical structure underlying a given sequence. The study of Reed and Johnson (1994) suggests that to appropriately test whether the complex statistical structure per se has been learned, instead of a random testing sequence, one should use training and testing sequences that differ only in second-order transitional probabilities but are identical in terms of first-order transitional probabilities and other simpler statistics (e.g., location frequency, transition frequency, reversal frequency, coverage, and transition usage). By controlling for the latter characteristics of both sequences, it can be ensured that the RT disruption across the sequences is due to acquiring the second-order transitional probability structure that changed from the first to the second sequence. It has also been shown that participants would less likely search for underlying structures if a sequence, compared with another, was subjectively perceived as more random, but, according to objective measures, was more structured (Wolford, Newman, Miller, & Wig, 2004). Considering these issues, in the present experiment, we deliberately avoided the use of fully random sequences; and, instead, we applied “equal probability” unstructured sequences, which were more controlled than the former ones. In addition, low-probability triplets being the major constituents of the unstructured sequences might have contributed to regarding these sequences as more random (Teigen & Keren, 2020).

4.8. Conclusions

The present experiment provides evidence that under implicit and incidental learning conditions, perceptual and cognitive processing continues to be influenced by a previously acquired predictable transitional probability structure even after that structure is removed. This implies that, due to the persistency of the acquired representations, unpredictable transitional probabilities are automatically processed according to these prior representations. However, after significant exposure to the unpredictable structure, the updating of prior representations becomes evident: Importantly, this process seems to require a longer stretch of time than that of the acquisition. Although the acquired representations are relatively persistent if the predictable structure is experienced first, protracted exposure to the unpredictable structure preceding the predictable one does not constrain the subsequent acquisition. Finally, the study also highlights the importance of carefully constructing the underlying structure of training and testing sequences in the investigation of statistical-sequence learning.

CRediT authorship contribution statement

Andrea Kóbor: Conceptualization, Methodology, Software, Project administration, Formal analysis, Funding acquisition, Writing - original draft.**Kata Horváth:**Conceptualization, Investigation, Project administration, Writing - review & editing.**Zsófia Kardos:**Conceptualization, Investigation, Writing - review & editing.**Dezso Nemeth:**Conceptualization, Resources, Supervision, Funding acquisition, Writing - review & editing.**Karolina Janacsek:**Conceptualization, Methodology, Software, Resources, Supervision, Writing - review & editing.

Acknowledgments

This research was supported by the National Brain Research Program (project 2017-1.2.1-NKP-2017-00002, PI: D. N.); the Hungarian Scientific Research Fund (OTKA FK 124412, PI: A. K., OTKA PD 124148, PI: K. J., OTKA K 128016, PI: D. N.); the IDEXLYON Fellowship of the University of Lyon as part of the Programme Investissements d'Avenir (ANR-16-IDEX-0005 to D. N.); and the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (to

A. K. and K. J.). The authors thank Balázs Török for providing custom-written scripts that generated the unstructured sequences, Borbála German for helping in data acquisition, and Zsófia Zavecz for providing helpful comments on the experimental design and on an earlier version of this paper. The authors also thank Barbara Tillmann, József Fiser, Gergő Orbán, Ilona Kovács, Noémi Éltető, and the reviewers for their illuminating comments and suggestions.

Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary material associated with this article contains Figs. S1 and S2. The raw data and the processed data of the study are also archived as Supplementary material. Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2020.104413.

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VII. Study 3: Does procedural learning remain intact when attention is divided between concurrent tasks and task goals?

Publication:

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), 1-14.

The **Supplementary Material** for the publication can be found in Appendix III.

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Divided attention does not affect the acquisition and consolidation of transitional probabilities

Kata Horváth[1,2,3], Csenge Török[2], Orsolya Pesthy[1,2], Dezso Nemeth[2,3,4]✉ & Karolina Janacsek[2,3,5]

Statistical learning facilitates the efficient processing and prediction of environmental events and contributes to the acquisition of automatic behaviors. Whereas a minimal level of attention seems to be required for learning to occur, it is still unclear how acquisition and consolidation of statistical knowledge are affected when attention is divided during learning. To test the effect of divided attention on statistical learning and consolidation, ninety-six healthy young adults performed the Alternating Serial Reaction Time task in which they incidentally acquired second-order transitional probabilities. Half of the participants completed the task with a concurrent secondary intentional sequence learning task that was applied to the same stimulus stream. The other half of the participants performed the task without any attention manipulation. Performance was retested after a 12-h post-learning offline period. Half of each group slept during the delay, while the other half had normal daily activity, enabling us to test the effect of delay activity (sleep vs. wake) on the consolidation of statistical knowledge. Divided attention had no effect on statistical learning: The acquisition of second-order transitional probabilities was comparable with and without the secondary task. Consolidation was neither affected by divided attention: Statistical knowledge was similarly retained over the 12-h delay, irrespective of the delay activity. Our findings can contribute to a better understanding of the role of attentional processes in and the robustness of visuomotor statistical learning and consolidation.

Statistical learning refers to the recognition and acquisition of probability-based associations among stimuli[1–5]. This learning process facilitates the efficient processing and prediction of environmental events and contributes to the acquisition of automatic behaviors and skills, such as language, dance, or typing. It can operate on visual or auditory input and with its help, we can process and acquire temporally or spatially distributed associations[5–12]. Statistical learning typically occurs incidentally and the acquired knowledge remains mostly implicit[13–15]. Although it is well-established that statistical learning can occur without intention, i.e., automatically, one of the main challenges in this field is to characterize how statistical learning and attention interact and how previous results concerning these two fundamental cognitive processes could be integrated [see[5,12]]. Whereas a minimal level of attention (to process the relevant stimuli) seems to be required for learning to take place[14,16], the effect of divided attention on statistical learning is still unclear and understudied[5]. Moreover, it remains unexplored how statistical knowledge acquired under divided attention is consolidated in the post-learning offline period. Therefore, here we aimed to test how divided attention affects statistical learning and the consolidation of the acquired statistical knowledge.

Divided attention is most often investigated by dual-task designs, that is, by testing whether performance is affected in the primary task of interest while participants simultaneously perform a secondary task[17,18]. Previous studies testing the effect of divided attention on statistical learning with dual-task designs led to mixed findings,

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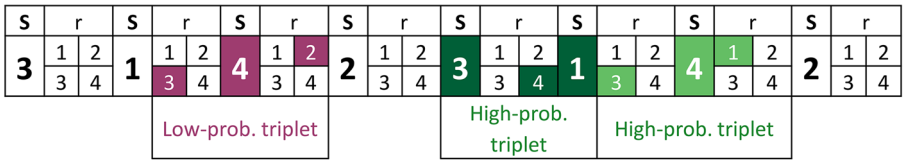
a



b

	Structure: S – r – S e.g., 3 – r – 1	Structure: r – S – r e.g., r – 4 – r
High-probability triplets (62.5% of all trials)	**e.g., 3 – 4 – 1 (50%)** Serial order information	**e.g., 3 – 4 – 1 (12.5%)**
Low-probability triplets (37.5% of all trials)	never occurring (always high)	**3 – 4 – 2 (12.5%)** **3 – 4 – 3 (12.5%)** **3 – 4 – 4 (12.5%)**

Statistical learning:
random high-probability
vs.
random low-probability

Figure 1. Stimulus structure and learning processes in the ASRT task (S—sequence, r—random). (**A**) As the ASRT task contains an alternating sequence structure (e.g., 2-r-3-r-1-r-4-r, where numbers correspond to the four locations on the screen and the 'r' represents randomly chosen locations out of the four possible ones), some associations of three consecutive trials (triplets) occur with greater probability (green) than others (purple). Within these triplets, due to the probabilistic structure, the third trial can be predicted by the first one with a certain probability, while the middle trial has no predictive value (i.e., second-order non-adjacent transitional probabilities). In the example above, the triplets 2-x-3, 3-x-1, 1-x-4, and 4-x-2 (where 'x' indicates the middle trial) are more probable. In contrast, e.g., 2-x-1, 1-x-3 or 3-x-2 would occur less probably. (**B**) We determined for each sequence and random trial whether it was the last trial of a high- or a low-probability triplet and, therefore, three different trials could occur: sequence (dark green, always high-probability), random high-probability (light green) and random low-probability (purple). Statistical learning is computed as the *difference* in responses to random high- vs. random low-probability trials. All sequence trials were excluded from the present analyses (for details see Methods).

although the following pattern seems to be emerging overall. When the secondary task is applied to the same stimulus stream and the processing of stimuli is intact (e.g., when participants are instructed to search for a given type of visual shape, while visual statistical learning takes place within the same stream of stimuli), statistical learning appears to be unaffected[14,18, cf. 19,20]. In contrast, when the secondary task operates on different stimuli than the primary task or some stimuli become unattended (e.g. completing a secondary working memory task at the same time as the visual statistical learning task), statistical learning appears to be hindered[16, cf. 19,21–24]. It is important to note, however, that the latter results might reflect the effect of selective instead of divided attention (i.e., when participants have to switch attention between attended and ignored stimuli[17]).

One of the most prominent task paradigms to investigate statistical learning are probabilistic sequence learning tasks[12,25–30]. In the present study, we employed a widely used visuomotor probabilistic sequence learning task, the Alternating Serial Reaction Time (ASRT) task[25–27] to assess visuomotor statistical learning. In this task, participants are asked to respond to a series of visually presented stimuli. The odd trials in the series follow a repeating serial order (a sequence), while the even trials are randomly selected, resulting in some runs of consecutive stimuli (second-order transitional probabilities) being more predictable than others. By cuing the sequence trials with different visual stimuli and instructing participants to learn their serial order while they *simultaneously* attend to and incidentally acquire the transitional probabilities in the same stimulus stream, the effect of divided attention on learning can be tested (see Figs. 1 and 2). That is, in this task design, cuing is assumed to divide attention between memorizing the repeating serial order of sequence trials and maintaining general task performance at the same time, while all stimuli remain attended. Although the effect of attention on statistical learning was not in the focus, so far, two studies investigated statistical learning in the cued version of the ASRT task comparing it to the uncued version. Whereas Nemeth et al.[26] showed enhanced statistical learning by cuing the sequence, Szegedi-Hallgató et al.[31] did not report such effect. Therefore, the question of whether sequence cuing, and thus divided attention, affects visuomotor statistical learning remains unclear.

Importantly, Nemeth et al.[26] and Szegedi-Hallgató et al.[31] used a self-paced task design, which enabled participants to spend as much time on the processing of and response to a given stimulus as they want. Such self-paced task designs can easily result in additional group differences and potential confounds as the acquisition process

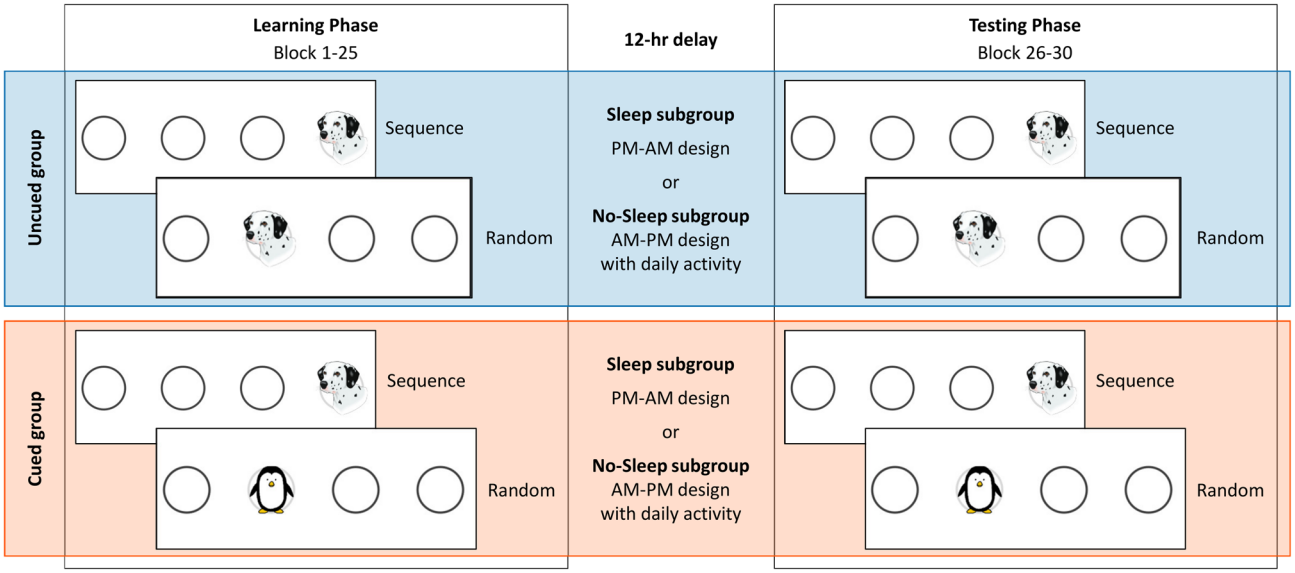


Figure 2. Design and procedure of the experiment. The ASRT task was administered in the experiment. In the cued version of the task (Cued group, orange panel), the regularity was marked by using different stimuli for the sequence trials (a dog's head) and the random ones (penguin). In the uncued version of the task (Uncued group, blue panel), sequence and random trials were not marked differently (all stimuli were presented by the dog's head). The Learning Phase (left column) consisted of 25 blocks, while the Testing Phase (right column) contained five blocks. The two sessions were separated by a 12-h delay. Based on the activity during the post-learning delay period, both main groups were divided into a Sleep (PM-AM design) and a No-sleep subgroup (AM-PM design). All participants performed the same ASRT task in the Testing Phase as in the Learning Phase.

itself may become longer in the group completing the cued task version (spending more time on processing the cued stimuli) compared with the group that performs the task without cues. Therefore, in the present study, we modified the task design to better serve our aims. Specifically, we used a fixed time window, in which participants could process and respond to the stimuli, so that the maximum amount of time participants could spend on each trial was equal in the conditions with vs. without the attentional manipulation. Additionally, the employed fixed paced timing was relatively fast compared to the self-paced or other fixed paced versions of task[32–34] to keep the attentional demand high in the Cued group. Due to these changes that were needed for the purpose of the present study, we refer to this task version as 'cued' instead of 'explicit' to differentiate it from the version used in previous studies.

As outlined above, previous studies have focused on how divided attention affects the acquisition of statistical knowledge, while how this knowledge is consolidated in the post-learning offline period that may contain sleep or daytime activities has been largely neglected. Typically—that is, without attentional manipulation—, statistical knowledge appears to be resistant to forgetting and interference, and the acquired knowledge is retained over an offline delay period[15,35–41]. Albeit a great body of research showed that sleep does not affect the consolidation of statistical knowledge, at least on the behavioral level[27,42–44], other studies argued for a beneficial effect of sleep in this process[45,46]. So far, to the best of our knowledge, only one study tested the consolidation of statistical knowledge that was acquired under a cuing manipulation. They showed retained statistical knowledge tested after a relatively short (1.5-h) delay period, irrespective of the delay activity (napping, quiet rest or active rest[35]). Nevertheless, these results were not directly contrasted with performance in an uncued condition, and attention was not manipulated systematically. Our study contributes to this body of research by contrasting statistical knowledge that was acquired with vs. without attentional manipulation (cuing of the sequence) and testing the consolidation of this knowledge after a 12-h offline period of sleep vs. daytime wakefulness.

Overall, we aimed to investigate the effect of divided attention on the acquisition and consolidation of second-order transitional probabilities. Attention was manipulated by cuing: half of the participants received the cued version of the ASRT task (Cued group) and were instructed to discover and learn the order of the cued sequence trials, while the other half completed the uncued version (Uncued group) without any additional task (see Figs. 1 and 2). Importantly, we employed a fixed time window for stimulus presentation and response in both groups to control the maximum amount of time they spend on each trial. The fixed paced timing also helped ensure that the attentional demand remained high in the Cued group. To examine how the delay activity during the post-learning offline period affects the consolidation of statistical knowledge, we divided the two main groups (Cued and Uncued) into further subgroups: half of each (Cued/Uncued) group slept during the 12-h delay period (Sleep subgroups), and the other half had normal daily activities (No-sleep subgroups). In addition, to provide a fuller picture of the acquired statistical knowledge, the *Inclusion–Exclusion task*[47,48] was administered: participants were asked to generate series of responses that followed the same regularities as the ASRT task (Inclusion condition) or one that was different from that (Exclusion condition). Based on Jacoby's process dissociation procedure[49],

Variable	Uncued group (N = 48)		Cued group (N = 48)	
	Sleep subgroup N = 24	No-sleep subgroup N = 24	Sleep subgroup N = 23	No-sleep subgroup N = 25
Age (year)	22.59 (4.52)	21.6 (2.57)	20.8 (1.15)	20.7 (1.62)
Education (year)	14.7 (2.43)	14.3 (2.18)	14.1 (1.09)	13.7 (2.16)
Handedness	19 right/4 left	19 right/5 left	19 right/4 left	19 right / 6 left
Gender	8 male/15 female	6 male/18 female	7 male/16 female	4 male / 21 female
Digit span task (short-term memory span, possible range: 3–9)	6.3 (1.26)	6.3 (0.87)	6.2 (0.97)	6.2 (0.93)
Counting span task (working memory span, possible range: 2–6)	3.5 (0.88)	3.6 (1.25)	3.9 (1.24)	3.3 (0.82)
ANT alerting attention (ms)	40.9 (23.0)	44.6 (27.96)	34.1 (18.80)	45.0 (29.45)
ANT orienting attention (ms)	31.4 (22.58)	26.4 (21.31)	38.8 (21.10)	41.1 (20.58)
ANT executive attention (ms)	88.4 (36.52)	77.5 (25.61)	84.83 (25.78)	89.1 (28.64)

Table 1. Demographic data of the four subgroups. Mean (SD) shown for age, education and standard neuropsychology tests assessing general cognitive performance. Ratio is presented for handedness and gender. *ANT*—Attention Network Test. Gender of one participant and handedness data from another participant are missing.

this task can help determine whether the acquired statistical knowledge remained implicit or participants could intentionally access and control this knowledge (for more details see the task description in the Methods section).

The effectiveness of the cuing manipulation was assessed by the RTs on the repeating sequence trials as well as with sequence reports obtained during the short breaks in the ASRT task. The acquisition of second-order transitional probabilities (that is, statistical learning) was measured on the random trials, for which no specific learning instructions were given in either group. We expected that statistical learning is not affected by divided attention, as achieved by the cuing manipulation, and statistical knowledge is retained during the post-learning delay period, irrespective of cuing (cued vs. uncued) and the delay activity (sleep vs. wake). We also expected that statistical knowledge remains implicit in both groups.

Methods

Participants. Ninety-eight healthy young adults participated in the experiment. One participant was excluded due to technical errors and another participant due to outlier performance on the ASRT task [raw reaction times (RTs) fell outside three SDs consequently for the random trial types in both experimental sessions, for more details see the Statistical Analysis section as well]. Thus, the final sample consisted of 96 adults, 48 in each group. To measure the effect of delay activity on consolidation, both groups were divided into two subgroups (for more details, see the Procedure section): Twenty-four participants were assigned to the Uncued Sleep subgroup, 24 participants to the Uncued No-sleep subgroup, 23 participants to the Cued Sleep subgroup and 25 participants to the Cued No-sleep subgroup.

All participants had normal or corrected-to-normal vision, none of them reported a history of any neurological and/or psychiatric condition and drug-use. Prior to their inclusion in the study, participants provided informed consent to the procedure as approved by the research ethics committee of Eötvös Loránd University, Budapest, Hungary. The study was conducted in accordance with the Declaration of Helsinki and participants received course credits for taking part in the experiment.

Handedness was measured by the Edinburgh Handedness Inventory[50]. In this test, the laterality quotient (LQ) is assessed, which can vary between −100 and 100 where −100 indicates complete left-handedness and 100 indicates complete right-handedness. Dichotomic handedness (left or right) was defined based on the LQ (values above zero were coded as right-handedness, and values below zero as left-handedness). General cognitive performance was measured by three widely used neuropsychological tests: participants completed the Digit Span task[51,52], the Counting Span task[53–56], and the Attentional Network Test[57]. The four subgroups did not differ in either of these measures (Table 1, all $ps > 0.088$).

Tasks. *Alternating serial reaction time (ASRT) task.* The ASRT task was used to measure the acquisition and consolidation of second-order transitional probabilities in the visuomotor domain. In this task, the target stimulus appeared in one of four horizontally arranged circles on the screen. Participants were instructed to respond with the corresponding key (Z, C, B or M on a QWERTY keyboard) when the stimulus occurred using their left and right middle and index finger. The presentation of the stimuli was determined by an eight-element sequence, within which sequence (S) and random (r) trials were alternating (Fig. 1A). One example of the sequence is 2-r-3-r-1-r-4-r, where numbers represent predetermined locations (1 denotes the leftmost position and 4 denotes the rightmost position) on the screen and r indicates randomly chosen locations out of the four possible ones. There are altogether six *unique* permutations of sequence order (1-r-2-r-3-r-4-r, 1-r-2-r-4-r-3-r, 1-r-3-r-4-r-2-r, 1-r-3-r-2-r-4-r, 1-r-4-r-3-r-2-r, 1-r-4-r-2-r-3-r). Please note that, for example, the sequences 1-r-2-r-4-r-3-r, 2-r-4-r-3-r-1-r, 4-r-3-r-1-r-2-r and 3-r-1-r-2-r-4-r consist of the same second-order transitional probabilities and

are therefore treated as identical. Participants received one of the six unique sequences in a pseudo-random and counterbalanced manner.

The alternating structure resulted in a *probability* structure within which some chunks of three consecutive trials (*triplets*) occurred with greater probability than others (Fig. 1A). Triplets formed the second-order transitional probability information of the task: The last trial (N) of a triplet could be predicted by the first one (N-2) with a certain probability, while the interleaving trial (N-1) did not have a predictive value. For example, in the example sequence above, when 1 (N) appeared in a sequence position, it always followed 3 in the N-2 position, and the interleaving trial (N-1) was randomly selected. However, if 1 appeared in a random position, the N-2 trial could be any of the four trials by chance. Triplets were considered *high-probability* if the third trial was predicted by the first trial with a greater probability (62.5% probability, Fig. 1B), whereas triplets were considered *low-probability* if the third trial was predicted by the first trial with a lower probability (12.5% probability). Accordingly, participants could extract and acquire the highly probable associations. Importantly, triplets were identified as a moving window throughout the entire stimulus set, that is, each trial was categorized as the last element of either a high- or a low-probability triplet, and it was also the first or the second trial of the following triplets. There were 64 possible triplets in the task: 16 of them were high-probability triplets and 48 were low-probability ones.

Trials could also be defined based on their *sequence* property according to the sequence structure: the last trial of a triplet could occur in a sequence position (S-r-S structure; e.g., 3-x-1 in the example above) or in a random one (r-S-r structure; e.g., 2-x-1 in the example above). All triplets with S-r-S structure occurred with high-probability due to the repetition of the sequence and these took up 50% percent of all triplets (Fig. 1B). In contrast, triplets with the r-S-r structure could occur with either high- (12.5% of all triplets) or low-probability (37.5% of all triplets). Therefore, each trial had a probability and a sequence property, and the last trial of each triplet could be divided into the following three trial types: sequence (always high-probability), random-high and random-low trials. The repeating sequence trials were used to create the additional learning task in the Cued group: these trials could be visually differentiated from the random ones (i.e., they were cued), and participants were instructed to learn their serial order (for more details, see Procedure). Consequently, triplets with S-r-S structure were contaminated by the intentionally acquired sequence knowledge in the Cued group where the last element of these triplets could be predicted based on the sequence order rule instead of the probability-based rule. Therefore, we focused only on the random high- and random low-probability trials because the sole difference between these was probability-based, that is, purely statistical in nature[31]. *Statistical learning* (the acquisition of second-order transitional probabilities) was measured as the *difference* between the responses to random high- vs. random-low probability trials (Fig. 1B[26,31,33–35]). Previously, studies investigating this measure have shown that learning already occurs after a short period of practice and the acquired knowledge is well-preserved[26,31,36]. The underlying learning process can be tracked on the level of electrophysiological signals as well[33–35].

Please note that previous studies mainly focused on the so-called triplet learning score calculated as the difference between the responses to high-probability versus low-probability trials without considering their sequence property. Thus, triplet learning score is not a pure measure of statistical learning because the probability information is contaminated by the serial order information. Despite this difference of whether or not sequence trials are included in the calculation of learning scores, the acquisition of second-order transitional probabilities (e.g., that '3-x-1′ is more probable than '2-x-1′ in the example sequence, Fig. 1) still contributes to both the triplet learning, and statistical learning scores. Importantly, statistical learning, triplet learning, and the acquisition of the sequence can be all separated from the so-called general skill learning that refers to general performance improvement as the task progresses (mainly due to improved visuomotor coordination) and affects the different trial types similarly[58]. In this study, we do not focus on these general changes in performance but only on statistical learning, that is, on the *difference* in responses to random high- vs. random low-probability trials.

Inclusion–exclusion task. The Inclusion–Exclusion task[47,48,59,60] is based on the well-established 'Process Dissociation Procedure' (PDP[49]) and it is typically used to separate incidental and intentional use of memory. Accordingly, this task was administered to reveal whether or to what extent the acquired *probability-based associations* became intentionally available in both the Uncued and Cued groups. To this end, first, participants were asked to generate a series of responses that followed the same regularities (that is, including both sequence and random trials) as the ASRT task (Inclusion condition). Second, they were asked to generate a new series of responses that followed different regularities (again, including both sequence and random trials) than the learned one (Exclusion condition). Both conditions contained four runs and participants used the same response buttons as in the ASRT task. Each run finished after 24 button presses, which was equal to three rounds of the eight-element alternating sequence. To measure performance, we computed the percentage of high-probability triplets generated in the Inclusion and Exclusion conditions separately. We then tested whether participants produced more high-probability triplets than it would have been expected by chance (which was 25%, see Procedure), and whether the percentage of high-probability triplets differed across (Inclusion/Exclusion) conditions or across groups.

Following the standard analysis and interpretation of the task outlined in previous studies[34,36,61], incidental use of knowledge (i.e., without intentional access to their knowledge) is sufficient to achieve good performance (that is, producing high-probability triplets *above* chance level) in the Inclusion condition. In contrast, good performance in the Exclusion condition (that is, producing high-probability triplets *at* or below chance level) requires intentionally accessible knowledge to exert control over their responses and generate a series of responses that is indeed different from what they practiced (i.e., intentionally exclude the acquired knowledge). Thus, if the acquired knowledge remained inaccessible to intentional control, we would expect high-probability triplets generated above chance level both in the Inclusion and Exclusion conditions. In contrast, intentional access to

the acquired knowledge would result in generating high-probability triplets above chance level in the Inclusion condition and at or below chance level in the Exclusion condition.

Procedure. The experiment consisted of two sessions to assess both learning and consolidation of the acquired knowledge. One block of the ASRT task contained 85 trials (stimuli). In each block, the eight-element alternating sequence repeated 10 times after five warm-up trials consisting only of random stimuli. The Learning Phase contained 25 blocks. Half of the participants received the uncued version of the ASRT task (*Uncued group*), while the other half performed a cued version of the task (*Cued group*) to induce divided attention. The Uncued group was informed that the aim of the experiment was to measure the effect of extended practice on motor performance, thus they were unaware of the sequence embedded in the task. In contrast, participants in the Cued group received information about the presence of a repeating sequence on the cued trials but not its length and were instructed to discover and intentionally memorize it as a secondary task. Nevertheless, participants were also instructed to pay attention to all stimuli and try to be equally fast and accurate on the pattern and random trials. In this version of the task, sequence and random stimuli were marked with different target pictures [dogs for sequence and penguins for random stimuli;[26,36]]. Consequently, the Uncued and Cued groups were named after the lack or presence of cues regarding the sequence. Please note that neither of the groups received any information regarding the second-order transitional probabilities of the task, therefore statistical learning is regarded as incidental in both groups.

To assess whether the learning situation remained incidental in the Uncued group, a short *questionnaire* was administered after the Testing Phase, similar to previous studies[27,62,63]. Participants were asked whether they observed any regularity in the task, and none of them reported anything regarding the embedded sequence or the learning situation. To ensure that the cuing manipulation was effective and the Cued group followed the instruction and learned the sequence order, a *post-block sequence report task* was administered after each block[33]. Participants were instructed to recall the order of the sequence trials (that was cued by the picture of a dog's head) and report the order three times (12 button presses).

We used a fixed inter-stimulus interval (ISI) to control for the maximum amount of time that the Cued and Uncued groups can spend on a given trial and therefore on the whole task. The timing of an experimental trial was the following: The duration of stimulus presentation was 500 ms (when participants were required to respond to the stimulus), then the four empty circles were presented for 120 m before the next stimulus appeared, thus, the total ISI was 620 ms. These values are defined based on previous studies investigating healthy young adults, where participants had an average response time under 450 ms at the beginning of the task and 430 ms by the end of the Learning Phase[27,63–65]. Moreover, by using a fast-paced fix ISI, we also aimed to keep the attentional demand high in the Cued group throughout the task, as compared with a slow-paced ISI or self-paced timing where participants typically learn the repeating sequence already within the first three-six blocks[26,32,33,35,62].

The Learning Phase was followed by a 12-h delay, thereafter the Testing Phase was administered, which contained five blocks of the ASRT task. In order to measure the effect of sleep on consolidation, a PM-AM vs. AM-PM design was used: during the delay, half of both Uncued and Cued groups slept (Sleep subgroups, PM-AM design) and the other half had normal daily activity (No-sleep subgroups, AM-PM design[27,66]). All PM sessions took place between 7 and 10 PM, and all AM sessions took place between 7 and 10 AM. Participants in the sleep subgroups slept on average 6 h (Uncued group: $M = 5.8$, $SD = 0.84$; Cued group: $M = 6.0$, $SD = 0.84$; $p = 0.511$). All participants were aware that they would perform the same task in the second experimental session (Fig. 2). Following the Testing Phase, both the Uncued and the Cued group performed the Inclusion–Exclusion Task.

Statistical analysis. Statistical analyses were based on previous studies[25,26,33,35,36,67] and were carried out using SPSS version 22.0 (SPSS, IBM).

Post-block sequence report task. This task was administered in the Cued group only. Performance on this task was used to test whether participants followed the instruction to learn the serial order of the cued sequence trials. Due to technical reasons, data from one participant in the Sleep subgroup was not recorded. First, the percentage of correct button presses (out of 12) was calculated after each block, then these were averaged across epochs (i.e., blocks of five, see below). These averaged values were submitted to mixed design ANOVAs separately for the Learning Phase and the 12-h post-learning offline delay to reveal whether participants followed the instruction and ascertain that the cuing manipulation was effective.

ASRT task. Epochs of five blocks were analyzed instead of single blocks: The Learning Phase consisted of five epochs, while the Testing Phase consisted of one epoch. On average, the Cued group showed slower RTs compared with the Uncued group, possibly as a result of the cuing manipulation (for more details see the Supplementary Materials). Hence, to ensure that potential between-group differences in statistical learning are not due to this group difference, we standardized the original RT values. To this end, first we transformed the data by dividing each participants' raw RT values for the random trials with their own average performance of the first epoch of the Learning Phase [for a similar approach see[68]]. In the next step, we multiplied all data by 100 for easier interpretability and presentation. This way, results could be interpreted in terms of percentages, where each participants' performance at the beginning of the Learning Phase was around 100% and changed as the task progressed. Following the transformation, the Uncued and Cued groups showed similar RTs (main effect of INSTRUCTION: $F(1, 92) = 0.011$, $p = 0.916$, $\eta_p^2 < 0.001$). Note that the results concerning raw RTs and accuracy can be found in the Supplementary Materials (Table S1 and Table S3, respectively, and Table S4 for the Bayesian analyses).

We calculated median RTs for correct responses only, for each participant and each epoch, separately for the random high- and random low-probability trial types. Then we calculated statistical learning scores as the *difference* between these two trial types, by extracting random high-probability trials from random low-probability ones. Larger scores indicated better learning performance. Due to the transformation procedure, these learning scores can be interpreted as percentages showing how much faster participants responded to the random high-probability trials compared with the random low-probability ones. These learning scores were submitted to mixed design ANOVAs to evaluate learning and consolidation of the acquired knowledge, respectively. Greenhouse–Geisser epsilon (ε) correction was used when necessary. Original *df* values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. LSD correction was used for pairwise comparisons and Cohen's *d* is reported as an effect size.

As we expected no change in performance as a function of cuing and/or the delay activity either during the Learning Phase or over the post-learning offline period, we conducted Bayesian ANOVAs to overcome the limitations of the frequentist approach (i.e., null-hypothesis significance testing[69,70]) and gain statistical evidence for the possible null-results. Bayes Factors (BF_{01}) were calculated using JASP (version 0.8.1.1, JASP Team, 2017). In these Bayesian ANOVAs, BF_{01} values reflect how well a model fits the data against the null model. The smaller the BF_{01} value is, the better the model predicts the data. BF_{01} value of the null model, which contains the grand mean only, is always 1 as it is compared to itself[71,72]. Additionally, we also present the evidence in the data for including a factor or an interaction of factors in a model quantified by $BF_{Exclusion}$ values (inverse of $BF_{Inclusion}$ values). $BF_{Exclusion}$ values reflect the change from prior inclusion odds to posterior inclusion odds and can be interpreted in the same ways as BF_{01} values (i.e., the smaller the value, the stronger the evidence for including the given factor). Bayesian analyses conducted on the standardized RTs as well as on the Inclusion–Exclusion task are presented after the standard null-hypothesis testing effects in the Results section below. For the sake of completeness, we also present the Bayesian analyses conducted on the raw RTs and the accuracy data in the Supplementary Materials (Discussion section and Table S4).

Inclusion–exclusion task. Twelve participants (two in the Uncued No-sleep subgroup, two in the Uncued Sleep subgroup, five in the Cued No-Sleep subgroup, and three in the Cued No-sleep subgroup) were excluded from these analyses as they did not follow the instructions in either the Inclusion or the Exclusion condition (e.g., not using every response buttons). Data from one participant in the Uncued Sleep subgroup is missing due to technical problems. To contrast performance against chance level, we calculated the percentage of high-probability triplets participants generated and subtracted the value of chance level (25%, percentage of the 16 high-probability triplets out of the 64 possible triplets). These scores were then submitted to a mixed design ANOVA. Since we did not expect any difference across the groups and the sample size was reduced here, a Bayesian mixed design ANOVA was also conducted and reported similarly as described above.

Results

Did the cuing manipulation successfully induce divided attention in the Cued group? To test whether the applied cuing manipulation was effective to induce divided attention in the Cued group, we conducted two different comparisons. First, we assessed responses for the *sequence trials*. Specifically, we compared performance on sequence trials with the average performance on random trials regardless of probability (i.e., averaged across random high- and random low-probability trials) across the four subgroups during the Learning Phase as well as over the 12-h post-learning offline period. Standardized RTs were analyzed here instead of raw RTs since general performance on the random trials was slowed down in the Cued group as reported above. Here we highlight the main result of interest only; all effects can be found in Table S2 of the Supplementary Materials. Importantly, in the Uncued group, we did not find any significant difference in RTs to sequence vs. random trials, whereas the Cued group showed faster responses to sequence trials compared with the random ones (Learning Phase: $p = 0.001$; over the 12-h delay: $p = 0.002$). This result demonstrates that the Cued group followed the cuing instruction and learned the repeating sequence trials, whereas this learning process was not apparent in the Uncued group. For more details, see also the Methods section and Figure S2 of the Supplementary Materials.

Second, we assessed the Cued group's performance on the *post-block sequence report task* to ensure that they indeed acquired the sequence order. A mixed design ANOVA was conducted on the percentage of correct button-presses in the Learning Phase with EPOCH as a within-subject factor (1–5) and SLEEP (Sleep vs. No-sleep) as a between-subject factor. The analysis revealed significant sequence knowledge (INTERCEPT: $F(1, 45) = 250.334$, $p < 0.001$, $\eta_p^2 = 0.848$). Furthermore, knowledge of the sequence order gradually increased over practice (significant main effect of EPOCH: $F(4, 180) = 19.078$, $p < 0.001$, $\varepsilon = 0.593$, $\eta_p^2 = 0.298$), while performance was similar between the Sleep and the No-sleep subgroups (main effect of SLEEP: $F(1, 45) = 0.02$, $p = 0.890$, $\eta_p^2 < 0.001$; EPOCH × SLEEP interaction: $F(4, 180) = 0.043$, $p = 0.974$, $\varepsilon = 0.593$, $\eta_p^2 = 0.001$; Fig. 3). To assess performance over the 12-h delay period, a similar ANOVA was conducted with EPOCH (the last epoch of the Learning Phase and the first epoch of the Testing Phase; thus, Epoch 5 vs. Epoch 6) as a within-subject factor and SLEEP (Sleep vs. No-sleep) as a between-subject factor. Again, significant sequence order knowledge was found (INTERCEPT: $F(1, 45) = 249.559$, $p < 0.001$, $\eta_p^2 = 0.847$), while performance did not differ either as a function of epoch (main effect of EPOCH: $F(1, 45) = 0.381$, $p = 0.540$, $\eta_p^2 = 0.008$) or delay activity (main effect of SLEEP: $F(1, 45) < 0.001$, $p < 0.995$, $\eta_p^2 < 0.001$; EPOCH × SLEEP interaction: $F(1, 45) = 0.068$, $p = 0.796$, $\eta_p^2 = 0.001$; Fig. 3). Overall, the post-block sequence report task provided further evidence that participants followed the cuing manipulation.

Do the uncued and cued groups show different statistical learning performance in the learning phase? We tested potential group differences in statistical learning by conducting a mixed design ANOVA on standardized RT data of the statistical learning scores (i.e., *difference* between random high- vs. random

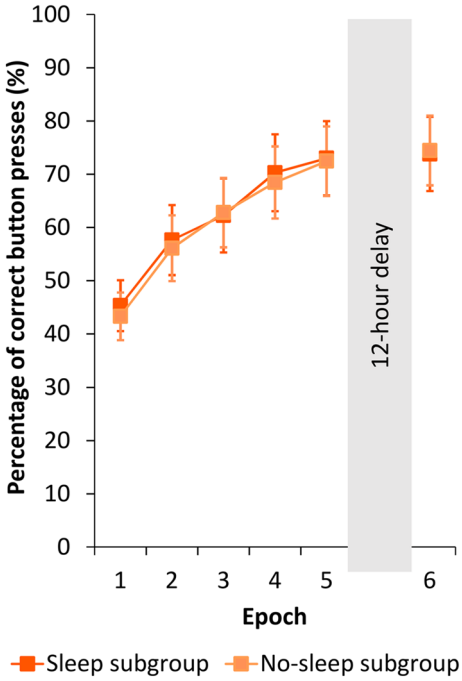


Figure 3. Performance of the Cued group in the post-block sequence report task over the Learning and Testing Phases. Participants were asked to provide 12 button presses, i.e., the four-element sequence three times, after each block of the ASRT task. Performance was defined as the percentage of correct button presses. The Sleep and No-sleep subgroups showed similar performance in the Learning Phase as well as after the post-learning offline period. While at the beginning of the Learning Phase participants performed around 40%, by the end of this session and during the Testing Phase they performed around 75% (i.e., they reported the sequence flawlessly two times out of three). We did not find any significant time of day or sleep-related effects during the Learning or Testing Phases, respectively. Error bars represent the standard error of the mean (SEM).

low-probability trial types) with EPOCH (1–5) as a within-subject factor and INSTRUCTION (Uncued vs. Cued) and SLEEP (Sleep vs. No-sleep) as between-subject factors. Note that, for the Learning phase, the Sleep vs. No-sleep subgroup comparison can reflect time of day effects rather than the effect of sleep per se as the Sleep subgroup was first tested in the evening and the No-sleep subgroup was first tested in the morning. The ANOVA revealed significant statistical learning (INTERCEPT: $F(1, 92) = 214.971$, $p < 0.001$, $\eta_p^2 = 0.700$), that is, participants responded faster to random-high probability trials compared with the random-low probability ones. The Uncued and Cued group did not differ significantly in the degree of statistical learning (main effect of INSTRUCTION: $F(1, 92) = 0.802$, $p = 0.374$, $\eta_p^2 = 0.011$), indicating that the cuing manipulation did not affect this type of learning. Irrespective of the group instruction, statistical knowledge increased as the task progressed (significant main effect of EPOCH: $F(4, 368) = 5.356$, $p < 0.001$, $\eta_p^2 = 0.055$). The EPOCH × INSTRUCTION interaction was not significant ($F(4, 368) = 0.671$, $p = 0.612$, $\eta_p^2 = 0.007$), suggesting that the trajectory of statistical learning was also independent of the cuing manipulation (see Fig. 4).

The Sleep and No-sleep subgroups, irrespective of the cuing, showed similar overall degree of statistical learning (main effect of SLEEP: $F(1, 92) = 0.288$, $p = 0.593$, $\eta_p^2 = 0.003$) and did not differ in their learning trajectory (EPOCH × SLEEP interaction: $F(4, 386) = 0.391$, $p = 0.815$, $\eta_p^2 = 0.004$). The INSTRUCTION × SLEEP interaction neither reached significance ($F(1, 92) = 2.800$, $p = 0.098$, $\eta_p^2 = 0.030$), indicating that the time of day, irrespective of the cuing manipulation, did not affect statistical learning performance. The EPOCH x INSTRUCTION × SLEEP interaction was not significant either ($F(4, 368) = 0.232$, $p = 0.920$, $\eta_p^2 = 0.003$), indicating that the trajectory of statistical learning was comparable in the four subgroups.

To confirm our interpretations, a Bayesian mixed design ANOVA and BF_{01} values were calculated for the Learning Phase. Our data favored the model containing only the factor of EPOCH ($BF_{01} = 0.0017$; $BF_{Exclusion} = 0.051$), providing further support to a similar statistical learning process regardless of whether or not the sequence was cued as well as of the time of day when learning occurred. All other BF_{01} values were higher than 1 (INSTRUCTION: $BF_{01} = 7.061$, $BF_{Exclusion} = 17.502$; EPOCH × INSTRUCTION: $BF_{01} = 3.860$, $BF_{Exclusion} = 103.581$; SLEEP: $BF_{01} = 6.507$, $BF_{Exclusion} = 16.079$; EPOCH × SLEEP: $BF_{01} = 5.640$, $BF_{Exclusion} = 159.104$; INSTRUCTION × SLEEP: $BF_{01} = 84.505$, $BF_{Exclusion} = 32.779$; EPOCH × INSTRUCTION × SLEEP: $BF_{01} = 479{,}224.597$, $BF_{Exclusion} = 187{,}945.864$).

Do the uncued and cued groups show different statistical performance over the 12-h offline period? A similar mixed design ANOVA on statistical learning scores was conducted to assess consolidation after the offline period with EPOCH (the last epoch of the Learning Phase and the first epoch of the Test-

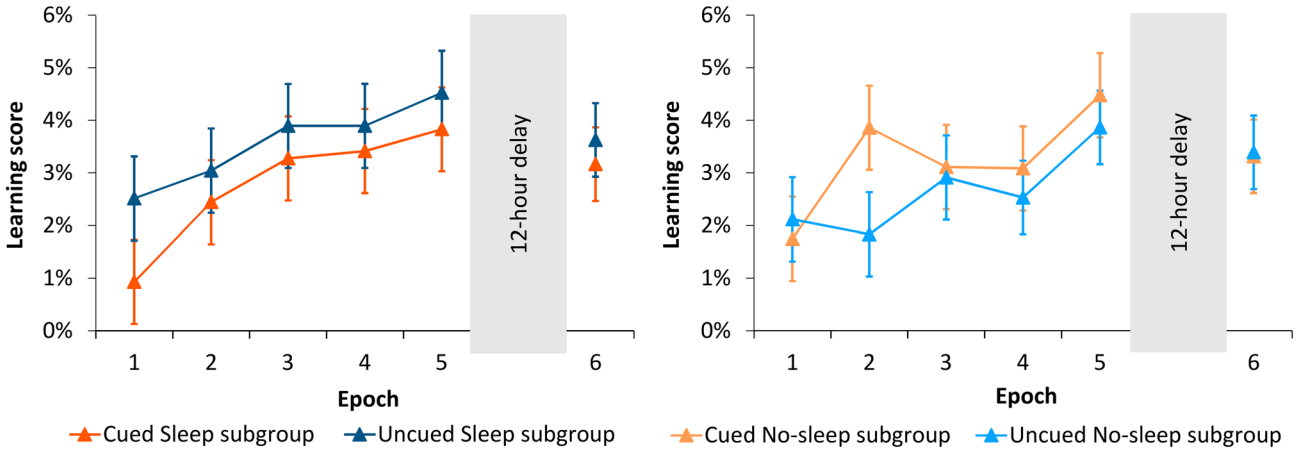


Figure 4. Statistical learning scores (i.e., the *difference* between RTs for random high- vs. random low-probability trials) over the Learning and Testing Phases. Left panel: Sleep subgroups within the Uncued and the Cued groups shown separately. Right panel: No-sleep subgroups within the Uncued and the Cued groups shown separately. The Uncued and Cued groups showed similar learning performance in the Learning Phase. Over the 12-h delay period, both the Uncued and Cued groups retained the acquired knowledge. We did not find any significant time of day or sleep-related effects during the Learning or Testing Phases, respectively. Error bars represent the SEM.

ing Phase; thus, Epoch 5 vs. Epoch 6) as a within-subject factor and INSTRUCTION (Uncued vs. Cued) and SLEEP (Sleep vs. No-sleep) as between-subject factors. Overall, participants showed knowledge of the statistical regularities (significant INTERCEPT: $F(1, 92) = 196.852$, $p < 0.001$, $\eta_p^2 = 0.681$). Similarly to the Learning Phase, the Uncued and Cued groups did not differ significantly in the amount of statistical knowledge (main effect of INSTRUCTION: $F(1, 92) = 0.083$, $p = 0.773$, $\eta_p^2 = 0.001$; Fig. 4). Statistical knowledge was retained over the offline period (main effect of EPOCH: $F(1, 92) = 2.704$, $p = 0.103$, $\eta_p^2 = 0.029$), irrespective of the cuing manipulation (EPOCH × INSTRUCTION interaction: $F(1, 92) = 0.055$, $p = 0.815$, $\eta_p^2 = 0.001$).

There were no significant differences in overall learning scores between the Sleep and No-sleep subgroups (main effect of SLEEP: $F(1, 92) = 0.002$, $p = 0.961$, $\eta_p^2 < 0.001$), irrespective of the cuing manipulation (INSTRUCTION × SLEEP interaction: $F(1, 92) = 0.620$, $p = 0.433$, $\eta_p^2 = 0.007$). Both the Sleep and No-sleep subgroups retained the acquired knowledge over the delay period (EPOCH × SLEEP interaction: $F(1, 92) = 0.002$, $p = 0.969$, $\eta_p^2 < 0.001$), similarly in the Uncued and Cued groups (EPOCH × INSTRUCTION × SLEEP interaction: $F(1,920) = 0.224$, $p = 0.637$, $\eta_p^2 = 0.002$, Fig. 4).

A Bayesian mixed design ANOVA and BF_{01} values were calculated for the learning scores in Epoch 5 and 6. This analysis provided further support for our results: our data favored the null model ($BF_{01} = 1$), suggesting the retention of statistical knowledge over the offline period regardless of the delay activity (Sleep vs. No-sleep) and of the cuing manipulation (Uncued vs. Cued; see Fig. 4). All other BF_{01} values as well as $BF_{Exclusion}$ values were higher than 1 (EPOCH: $BF_{01} = 1.551$, $BF_{Exclusion} = 3.957$; INSTRUCTION: $BF_{01} = 5.109$, $BF_{Exclusion} = 12.780$; EPOCH × INSTRUCTION: $BF_{01} = 37.411$, $BF_{Exclusion} = 28.492$; SLEEP: $BF_{01} = 5.438$, $BF_{Exclusion} = 12.909$; EPOCH × SLEEP: $BF_{01} = 23.999$, $BF_{Exclusion} = 33.257$; INSTRUCTION × SLEEP: $BF_{01} = 88.567$, $BF_{Exclusion} = 48.228$; EPOCH × INSTRUCTION × SLEEP: $BF_{01} = 8951.745$, $BF_{Exclusion} = 1262.395$).

Was the acquired knowledge intentionally accessible? To test whether the acquired probability-based information remained implicit or became intentionally accessible, the *Inclusion–Exclusion task* was administered in both groups (see Methods) after the ASRT task of the Testing Phase. Data were analyzed in a mixed design ANOVA with CONDITION (Inclusion vs. Exclusion) as a within-subject factor and INSTRUCTION (Uncued vs. Cued) and SLEEP (Sleep vs. No-sleep) as between-subject factors. The significant main effect of INTERCEPT ($F(1, 79) = 76.104$, $p < 0.001$, $\eta_p^2 = 0.491$) revealed that, overall, participants generated high-probability triplets above chance level, which was 25%. The main effect of CONDITION revealed a slight trend towards more high-probability triplets being generated in the Inclusion than in the Exclusion condition ($F(1, 79) = 3.205$, $p = 0.077$, $\eta_p^2 = 0.039$). The main effect of INSTRUCTION ($F(1, 79) = 0.254$, $p = 0.616$, $\eta_p^2 = 0.003$) and the CONDITION × INSTRUCTION interaction ($F(1, 79) = 0.901$, $p = 0.345$, $\eta_p^2 = 0.011$) were not significant, suggesting that the cuing manipulation did not have an overall effect on the proportion of high-probability triplets generated in the Inclusion and Exclusion conditions (see Fig. 5), even despite the fact that the Cued group gained explicit knowledge about the order of the cued repeating sequence as evidenced by the results of the post-block sequence reports (see the first subsection of the Results).

The main effect of SLEEP was not significant ($F(1, 79) = 0.254$, $p = 0.616$, $\eta_p^2 = 0.054$). The CONDITION × SLEEP interaction, however, revealed a significant group difference between the Inclusion and Exclusion conditions ($F(1, 79) = 4.687$, $p = 0.033$, $\eta_p^2 = 0.056$). Pairwise comparisons showed that the Sleep subgroups altogether (i.e., combined across the Cued and Uncued groups) generated less high-probability triplets in the Exclusion condition compared with the Inclusion condition ($p = 0.007$, $d = 0.09$), while the No-sleep subgroups performed similarly in the two conditions ($p = 0.791$, $d = 0.02$). The INSTRUCTION × SLEEP interaction also

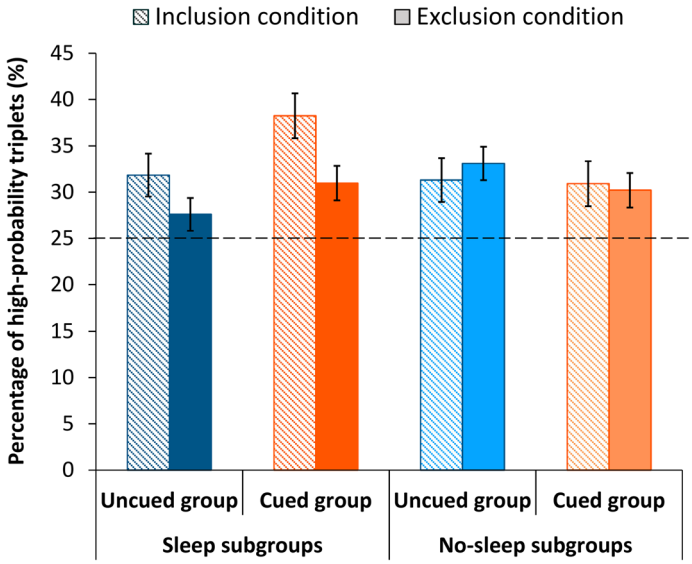


Figure 5. Percentage of high-probability triplets generated in the Inclusion and the Exclusion conditions by the four subgroups. Dashed horizontal line at 25% marks chance-level performance. Overall, participants performed above chance level both in the Inclusion and Exclusion conditions. The Sleep subgroups altogether (combined across the Uncued and Cued groups) generated a slightly different percentage of high-probability triplets in the Exclusion and Inclusion conditions, while the No-sleep subgroups performed at similar levels in the two conditions. This pattern seemed somewhat stronger for the Cued Sleep subgroup compared with the Uncued Sleep group. These group differences, however, were not supported by the Bayesian ANOVA. Error bars represent the SEM.

revealed a significant effect ($F(1, 79) = 4.419$, $p = 0.039$, $\eta_p^2 = 0.053$). Pairwise comparisons on the *combined* performance in the Inclusion and Exclusion conditions showed that while the Sleep and No-sleep subgroups within the Uncued group performed comparably ($p = 0.253$, $d = 0.05$), the Cued Sleep subgroup generated slightly more high-probability triplets compared with the Cued No-sleep subgroup ($p = 0.074$, $d = 0.10$) and the Uncued Sleep subgroup ($p = 0.030$, $d = 0.12$), as well. The No-Sleep subgroups also performed similarly ($p = 0.455$, $d = 0.03$). This pattern seems to be driven mainly by the Cued Sleep subgroup generating more high-probability triplets in the Inclusion condition than any other subgroups (see Fig. 5), although the CONDITION × INSTRUCTION × SLEEP interaction did not reach significance ($F(1, 79) = 0.009$, $p = 0.926$, $\eta_p^2 < 0.001$). Overall, these results point towards that the Sleep subgroups could intentionally access and control the acquired knowledge to a certain level, while the No-sleep subgroups could not. This pattern seemed to be slightly stronger for the Cued Sleep subgroup compared with the Uncued Sleep subgroup. Nonetheless, as the effect sizes for the pairwise comparisons are small, these results should be treated with caution. Finally, all subgroups still performed above chance-level in the Exclusion condition, suggesting that none of them could exert full control over the acquired knowledge as required by the task instructions.

A Bayesian mixed design ANOVA was also conducted for this data, revealing that the best fitting model contains only the grand mean (BF_{01} of the null model = 1.000; CONDITION $BF_{01} = 1.353$, $BF_{Exclusion} = 2.165$; INSTRUCTION $BF_{01} = 3.500$, $BF_{Exclusion} = 5.416$; CONDITION × INSTRUCTION $BF_{01} = 12.604$, $BF_{Exclusion} = 6.345$; SLEEP $BF_{0}1 = 4.784$, $BF_{Exclusion} = 4.585$; CONDITION × SLEEP $BF_{01} = 1.353$, $BF_{Exclusion} = 1.838$; INSTRUCTION × SLEEP $BF_{01} = 12.454$, $BF_{Exclusion} = 3.735$; CONDITION × INSTRUCTION × SLEEP $BF_{01} = 28.641$, $BF_{Exclusion} = 5.918$). Thus, the Bayesian analysis suggests that the delay activity related findings of the mixed-design ANOVA reported above are not reliable, possibly due to the low sample size, and therefore should be treated with caution.

Discussion

The goal of the present study was twofold. First, we tested how divided attention affects the acquisition of second-order transitional probabilities in the same stimulus stream. Second, we investigated how the post-learning offline period affects the acquired statistical knowledge with a particular focus on the role of the delay activity (sleep vs. wake). Performance was measured by a probabilistic sequence learning (namely, the ASRT) task within which the sequence was cued for one half of the participants (Cued group) and uncued for the other half (Uncued group). We controlled for the time on task with a fast-paced fixed inter-stimulus interval, which also served to maintain the attentional demand in the cued version. The learning phase was followed by a 12-h post-learning offline period, which contained sleep for half of the groups (Sleep subgroups) and normal daily activity for the other halves (No-sleep subgroups), to measure consolidation of the acquired statistical knowledge. Compared with the Uncued group, the Cued group responded faster on the cued sequence trials than on the random ones, independent of trial-probability. Furthermore, the post-block sequence report task, administered in the Cued group only, showed that participants acquired the sequence order. These results provide evidence that participants

in the Cued group followed the instruction and the cuing manipulation was successful in inducing a divided attention condition.

Our results regarding statistical learning performance revealed that the learning process was not sensitive to the cuing manipulation: The Cued and Uncued groups showed similar learning performance. The comparison of the Sleep and No-sleep subgroups in the Learning Phase could have reflected time of day related effects rather than the effect of sleep per se due to the applied PM-AM/AM-PM design. Nevertheless, we did not find such a time of day related group difference. After the 12-h post-learning offline period, all subgroups showed similarly retained statistical knowledge, suggesting that the consolidation was also independent of the cuing manipulation and was resistant to the delay, irrespective of the post-learning delay activity (sleep vs. wake). These results were further supported by the Bayesian analyses. Moreover, the analysis of raw (i.e., non-standardized) RTs as well as of the accuracy data also yielded the same patterns. The Inclusion–Exclusion task revealed that both the Cued and Uncued groups could comparably generate the knowledge on the structure of the task, while neither could intentionally access and control this knowledge. Sleep during the offline delay seemed to have a slightly beneficial effect on the latter process; nonetheless, this result should be treated with caution as the sample size was reduced here, and the Bayesian analysis did not support the finding.

In line with our hypothesis, the manipulation of attention had no effect on the *acquisition* of statistical knowledge, either as measured by RT learning scores (the primary measures for our analyses, see also Table S1 and Table S4 of Supplementary Materials) or by accuracy learning scores (see Table S3 and Table S4). So far, studies investigating statistical learning in the ASRT task with and without a cued sequence revealed mixed results. Nemeth et al.[26] showed enhanced statistical learning performance, while in the study of Szegedi-Hallgató et al.[31] performance was similar across the cued and uncued groups. The reason for these mixed results is unclear. One possible explanation is that the self-paced timing of the task enabled participants to spend different time on the task, potentially leading to enlarged individual differences within as well as across studies. Nevertheless, it is important to note that although these studies used a similar cued version of the ASRT task, they did not aim to systematically manipulate attention processes. We established changes in the experimental design so that it better suits the goals of the present study. First, we aimed to control for the time on task by using a fixed timing, so that the maximum amount of time that participants could spend on a given trial (and consequently on the task as a whole) was the same for the Uncued and Cued groups. Second, we applied a fast paced timing to avoid the automatization of sequence knowledge[32,33,35] and keep the attentional demand high in the Cued group. Overall, our findings suggest that the acquisition of second-order transitional probabilities is not affected by divided attention in the ASRT task even when we control for the timing of the task.

Previous studies investigating the effect of a secondary task on statistical learning yielded inconsistent findings: Some conclude that statistical learning is resistant to a dual task manipulation[14,18–20,73], while in other cases degraded performance is observed[16,19,21–24]. Importantly, statistical learning in the language domain seems to be more affected by a secondary task[16,22, cf. 23], compared with statistical learning in the visuomotor domain[14,18–20], in line with our results. However, as already mentioned in the Introduction, some of these studies used a secondary task related to a second stimulus stream resulting in a selective attention manipulation where good performance on both tasks can be achieved if attention is switched between the two tasks, potentially affecting the stimulus processing, as well[17,74,75]. In the present experiment, we chose the cuing of the repeating sequence embedded in the same stimulus stream as the probability-based associations, while all stimuli of that stream are similarly processed, and attention is divided between the cued and the uncued stimuli. Based on our and the previous results[14,18,20], we conclude that visual statistical learning is not affected by divided attention.

Regarding the *consolidation* of statistical knowledge, on the one hand, we found that the acquired statistical information both with and without the cuing manipulation was comparably retained during the 12-h post-learning offline period. The consolidation of (pure) statistical knowledge has received relatively little empirical attention so far[15,46,76]. Previous studies that used the uncued version of the ASRT task only focused on the so-called triplet learning measure (for more details see Task section[36,37,41,42,66,77–79]), which, although somewhat contaminated with sequence information, seemed to be stable during the offline delay such as statistical learning. Consolidation of *pure* statistical knowledge in the cued version of the ASRT task has been investigated in Simor et al.'s study[35], showing no change in statistical knowledge over a 1.5-h long offline delay. Our findings are consistent with these studies and our hypothesis, revealing reliably retained statistical knowledge during a 12-h offline period, irrespective of whether learning occurred with or without divided attention. These results were further confirmed by the Bayesian analysis, the raw (i.e., non-standardized) RT data and the accuracy data.

We also examined the role of delay activity (sleep vs. wake) in the consolidation of statistical knowledge, and found that sleep did not have a differential effect on performance, as expected based on previous studies[27,35,42,80,81]. The acquired knowledge was similarly retained, irrespective of the delay (sleep vs. wake) activity. Although the analysis of accuracies yielded improved consolidation during sleep as opposed to a wake offline period (see Results section and Table S3 of Supplementary Materials), this result was not confirmed by the Bayesian analysis (Discussion section and Table S3 in the Supplementary Materials). Furthermore, in line with our main results on standardized RTs, the analysis of raw RTs yielded evidence for a sleep-independent consolidation (for the frequentist analysis, see Introduction section, Figure S1 and Table S1; for the Bayesian analysis, see Discussion section and Table S4 in Supplementary Materials). Altogether, our results suggest that, at least in the visuomotor domain, statistical knowledge is retained over a 12-h delay period, irrespective of divided attention and delay activity (sleep vs. wake).

Finally, to investigate whether the cuing manipulation and the delay activity affected the intentional access to and control over the acquired statistical knowledge after the ASRT task in the Testing Phase, the *Inclusion–Exclusion task* adapted from Jacoby's Process Dissociation Procedure[36,48,49] was used. This measure revealed that the delay activity had a greater effect on performance than the cuing manipulation (cf. SLEEP × CONDITION interaction vs. INSTRUCTION × SLEEP interaction). The Sleep subgroups (combined across the Cued and

Uncued groups) could intentionally access and control the acquired knowledge to a certain level, while the No-sleep subgroups could not. This pattern seemed somewhat stronger for the Cued Sleep subgroup compared with the Uncued Sleep as well as the Cued No-Sleep subgroup. Importantly, as the Bayesian analysis did not confirm these results and sample size was reduced in this task (see the Inclusion–Exclusion task subsection of Statistical analysis), these conclusions should be treated with caution. The lack of a significant INSTRUCTION × CONDITION interaction suggests that even though the Cued group intentionally learned the repeating sequence order (see the post-block sequence report task and the analysis of sequence trials), this did not improve the access to their statistical knowledge. Overall, results suggest that none of the groups could exert intentional control over the acquired probability-based knowledge.

The present study is not without limitations. First, opposing the established divided attention designs where the primary and secondary tasks can be tested both together and independently, the secondary task (i.e., the intentional acquisition of the sequence order) could not be tested separately in the present experiment. The main goal of the present study was to keep all stimuli attended and rule out that statistical learning performance is affected merely due to altered stimulus processing [cf. 17]. To this end, we chose an experimental design that, although did not allow us to measure the secondary task separately, bore the benefit that both tasks took place within the same stimulus stream. Second, the applied fixed paced timing could have resulted in biased RTs by disincentivizing participants to respond as fast as possible. Nevertheless, we still observed faster RTs for the sequence trials compared with the random ones in the Cued group (cf. Figure S2), suggesting that the task settings were still well-suited to assess the effect of cuing on performance. Third, the applied PM-AM/AM-PM design inevitably created group differences regarding the time of day when acquisition and testing took place. Although this difference could have confounded the present results, the lack of Sleep versus No-sleep subgroup differences in statistical learning or consolidation speaks against this scenario.

In summary, the present study showed that divided attention does not affect the acquisition and consolidation of second-order transitional probabilities in the visuomotor domain. Statistical learning successfully took place and the acquired knowledge was retained over the 12-h post-learning offline period, irrespective of whether or not participants paid attention to the cued sequence embedded in the same stimulus stream. Sleep seems to have no superiority compared with a wake delay activity in these processes. Overall, our findings provide deeper insights into the potential roles of divided attention and the post-learning delay activity (sleep vs. wake) in the acquisition and consolidation of statistical knowledge and highlight the robustness of these processes.

Data availability

All data are available on the following online repository: https://osf.io/b68pg/?view_only=c22678446d0f47bfaa78d051f00e0af9.

Received: 18 February 2020; Accepted: 24 November 2020
Published online: 31 December 2020

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Acknowledgements

This research was supported by the National Brain Research Program (2017-1.2.1-NKP-2017-00002 to D.N.); Hungarian Scientific Research Fund (NKFIH OTKA PD 124148 to K.J., NKFIH OTKA K 128016), Janos Bolyai Research Fellowship of the Hungarian Academy of Sciences (to K.J.), the ÚNKP-19-3 New National Excellence Program of the Ministry for Innovation and Technology (to K.H.), and the IDEXLYON Fellowship of the University of Lyon as part of the Programme Investissements d'Avenir (ANR-16-IDEX-0005 to D.N.). D.N. is thankful for the support of IMÉRA. The authors thank the help of Balázs Török in data acquisition and data analysis.

Author contributions

K.H. collected data, administered the project, did formal data analysis, wrote and revised the manuscript. C.T. collected data, administered the project, did formal data analysis, and wrote the manuscript. O.P. collected data and wrote the manuscript. D.N. provided financial and theoretical support, conceptualized and designed the study, supervised data analyses, wrote and revised the manuscript. K.J. created experimental software, conceptualized and designed the study, did formal data analysis, supervised data analyses, wrote and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-020-79232-y.

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VIII. Study 4: How does response inhibition influence the rewiring of automatic behaviours?

Publication:

Horváth, K., Nemeth, D., & Janacsek, K. (2022). Inhibitory control hinders habit change. *Scientific Reports*, *12*(1), 1-11.

The **Supplementary Material** for the publication can be found in Appendix IV.

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Inhibitory control hinders habit change

Kata Horváth[1,2,3,4], Dezso Nemeth[2,3,5,7]✉ & Karolina Janacsek[2,6,7]✉

Our habits constantly influence the environment, often in negative ways that amplify global environmental and health risks. Hence, change is urgent. To facilitate habit change, inhibiting unwanted behaviors appears to be a natural human reaction. Here, we use a novel experimental design to test how inhibitory control affects two key components of changing (rewiring) habit-like behaviors in healthy humans: the acquisition of new habit-like behavior and the simultaneous unlearning of an old one. We found that, while the new behavior was acquired, the old behavior persisted and coexisted with the new. Critically, inhibition hindered both overcoming the old behavior and establishing the new one. Our findings highlight that suppressing unwanted behaviors is not only ineffective but may even further strengthen them. Meanwhile, actively engaging in a preferred behavior appears indispensable for its successful acquisition. Our design could be used to uncover how new approaches affect the cognitive basis of changing habit-like behaviors.

Our automatic, habitual behaviors are constantly challenged. The ongoing threats from environmental and health disasters[1,2] force us to alter dangerous and unsustainable behaviors, and to replace them with safer, sustainable ones. To achieve this, it is crucial to understand how habits form and change in the healthy human mind[3].

Habits are traditionally defined as automatic stimulus–response links that are insensitive to the outcome value of the response (as opposed to goal-directed behaviors), by non-human animal studies[4,5]. Previous research aimed at directly translating this definition to measuring habits in humans has repeatedly failed (for recent successful attempts, see[6,7]). Alternatively, human habits can be defined as more complex behaviors that are characterized by a collection of behavioral attributes: they are acquired via associative learning processes gradually over an extended period of practice, often without conscious awareness, and once developed, they can be performed with little thought or attention (i.e., automatically; for more details see the "Behavioral and neural characteristics of habit learning across human and animal studies" section in the Supplementary Information)[8–13]. During habit change, new associations are learned to replace old ones, suggesting that overcoming old habits and developing new habits share the same learning process[14,15]. Aspects of habit change have been widely studied in clinical and health settings (e.g., addiction), in non-human animals, and in relation to reward-related behavior (e.g., extinction and counterconditioning)[16,17]. This research has extensively characterized the computational and neural underpinnings of how simple stimulus–response(–reward) associations contribute to habit formation and change. However, it remains poorly understood how habit change occurs in healthy humans when more complex associations (i.e., when not only the current stimulus influences the response but a sequence of preceding stimuli) are learned and modified without explicit rewards[18]. These features more closely resemble habit change in daily life; therefore, identifying the cognitive changes that occur during habit change in these contexts could significantly broaden our understanding in this field.

A recent study using self-reported measures in healthy individuals found that increasing the frequency of new, sustainable behaviors (i.e., forming sustainable habits) was perceived to be more feasible than reducing old, unsustainable ones[19]. When participants imagined reducing unsustainable behaviors, the right dorsolateral prefrontal cortex—a key brain region for inhibitory-control processes—was activated. This finding suggests that inhibiting old, unsustainable behaviors may be a natural reaction when attempting to change habits. Research on

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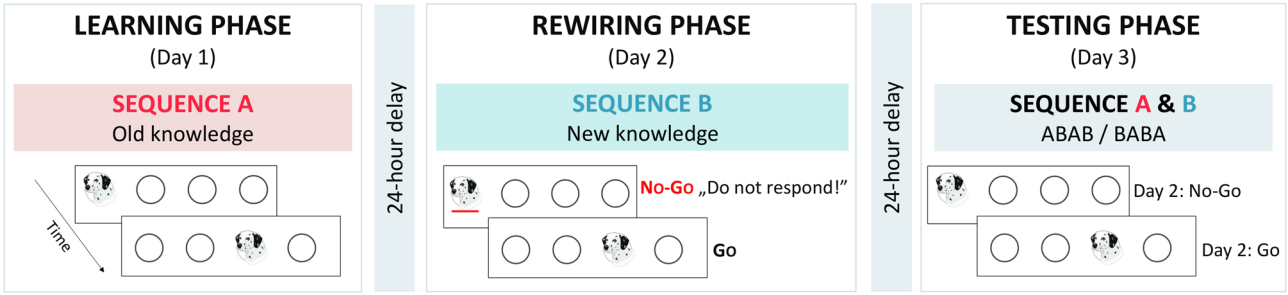

Figure 1. Design of the experiment. The experiment consisted of three phases, each separated by 24-h delays. During the Learning phase, participants extensively practiced a four-choice visuomotor reaction time task over 3600 trials, divided into three periods. In this task, a stimulus appeared in one of four horizontally arranged circles on the screen, and participants were asked to respond as quickly and accurately as they could using a response box. The associations of Sequence A (referred to as old knowledge) were acquired in this phase. Then during the Rewiring phase, a structural change was introduced to the task with Sequence B to prompt the rewiring of the old knowledge by acquiring the associations of this new sequence (referred to as new knowledge). Additionally, to engage participants' inhibitory control processes in this phase, they were asked to suppress their responses on some trials (stimuli underlined with a red line during the task, No-go trials), but could respond on other (Go) trials. This phase also consisted of 3600 trials, divided into three periods. In the Testing phase, using a shorter version of the task, knowledge of both sequences was probed in a counterbalanced order (ABAB or BABA on the figure, where A and B refer to the sequence used in the Learning and Rewiring phases, respectively). Here, responses were allowed on all trials, including previously suppressed No-go trials, to assess the effect of inhibitory control on rewiring. The stimulus was taken from the public domain (retrieved on 26/09/2017 from: www.pixabay.com).

habit change in everyday settings has also implicated the role of effortful inhibition and self-control in overcoming unwanted behaviors[18,20]. Importantly, however, how inhibitory control—the ability to suppress prepotent but unwanted actions, thoughts, or emotions[21,22]—affects habit change when complex associations need to be modified has not yet been directly probed in a controlled experimental setting in healthy humans.

Here we created a novel experimental design to test how inhibitory control affects two key components of changing habit-like behaviors: the acquisition of new complex associations and the simultaneous unlearning of old ones, in a neutral environment (i.e., without explicit rewards). Learning processes were examined via *rewiring*, whereby structural changes in the experimental task promoted the acquisition of new associations in place of old ones[23]. To test the rewiring of the initially acquired knowledge (henceforth referred to as old knowledge), we first needed to ensure that this knowledge was indeed acquired. This was assessed during the Learning phase, where 33 healthy young adults underwent an extensive practice on a visuomotor, four-choice reaction time task[24–26] (Fig. 1). Unbeknownst to them, location of the visual stimuli followed a predetermined sequential order that alternated with randomly chosen locations, resulting in some runs of three consecutive trials (referred to as triplets) being more probable than others. This enabled us to track the initial acquisition of complex associations continuously.

This old knowledge was then challenged in the Rewiring phase, in which a structural change was introduced to the task. Seventy-five percent of originally high-probability triplets became low-probability (denoted as HL trials) and were replaced by new high-probability triplets (that were originally low-probability, denoted as LH trials; see Fig. 2a and, for further details, the "Supplementary methods" section in the Supplementary Information), prompting the rewiring of the old knowledge. Thus, participants needed to unlearn most of what they acquired in the Learning phase as it was no longer relevant, and simultaneously acquire new associations from the partially changed sequence (henceforth referred to as new knowledge). Additionally, participants were asked to actively inhibit responses on some trials to engage their inhibitory control processes in this phase[27,28]. Then, both the old and new knowledge was assessed in the Testing phase. Here, responses were allowed on all trials, including those in which participants inhibited their responses during rewiring, to probe how inhibition affected their (un)learning processes. Using this carefully controlled experimental setting, we were able to directly examine how inhibitory control affects the (un)learning of complex associations that underlie automatic habit-like behaviors in healthy adults.

Initial acquisition and subsequent unlearning of associations that were no longer relevant due to the structural change in the task. Learning successfully occurred in the Learning phase (Fig. 3a, circled area): participants showed increasingly higher learning scores ('LL minus HL', underlined letters indicating the triplet probabilities of the current comparison), reflecting faster responses to trials that were high-probability in Sequence A compared to low-probability ones (for raw RTs see Fig. S1a). This old knowledge was then partially unlearned during the Rewiring phase (Fig. 3a, non-circled area), in which originally high-probability trials became less probable ('LL minus HL'; thus, both trial types compared were low-probability in Sequence B). The different time course of (un)learning across the two phases is indicated by the significant Phase × Period interaction ($F(2, 60) = 5.70$, $p = 0.005$, $\eta_p^2 = 0.160$). Specifically, participants gradually acquired the associations of Sequence A (Period 1 vs. Period 3: $p = 0.002$, Cohen's $d = 0.60$, $BF_{01} = 0.059$), with learning scores differing signifi-

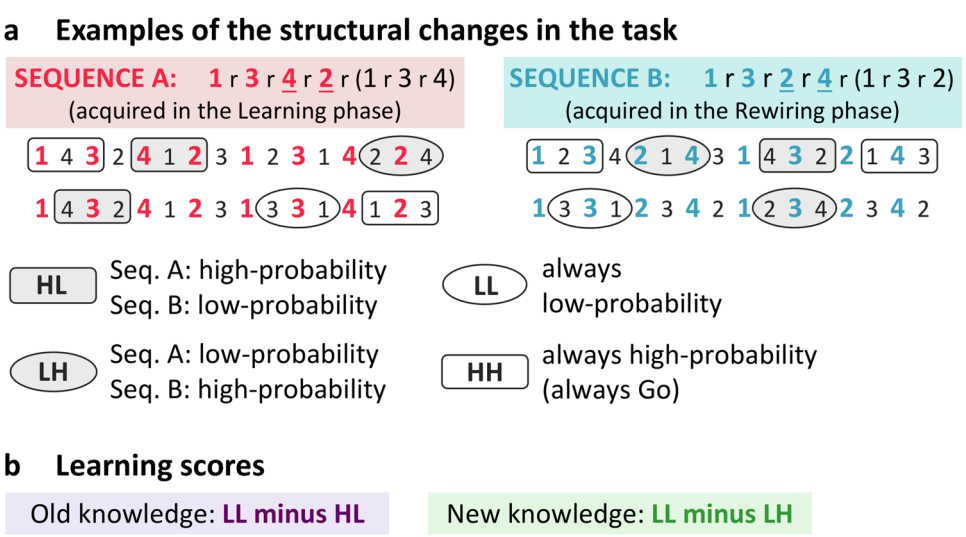

Figure 2. Task structure and measures of learning in the experiment. (**a**) Locations of the visual stimuli followed a predetermined sequential order (1 through 4 on the figure indicate the four horizontally arranged locations on the screen) that alternated with randomly chosen locations (indicated by r) out of the four possible ones. Example sequences are shown on the figure; overall, pairs of six unique sequences were used in a counterbalanced order. Due to the alternating sequence structure, some runs of three consecutive trials were more probable than others (referred to as high- vs. low-probability triplets, respectively)[29]. An example of the difference between Sequence A and Sequence B used in the Learning and Rewiring phases, respectively, is shown by the underlined numbers. Due to this structural change in the task, the probability of some triplets changed from the Learning phase to the Rewiring phase: 75% of the initially high-probability triplets became low-probability (HL trials; thus, the first letter refers to the triplet probability in Sequence A, while the second letter refers to the probability of the same triplet in Sequence B) and were replaced by new high-probability triplets that were initially low-probability (LH trials). Additionally, the occurrence probability of some triplets remained constant: either being low-probability (LL trials) or high-probability (HH trials) in both phases (for further details see "Methods" section). (**b**) Learning scores were calculated as differences in response times to trials with changed (LH or HL) versus unchanged occurrence probabilities (LL or HH). This enabled us to assess how participants initially acquired the associations of Sequence A, and then updated their knowledge when practicing Sequence B. For example, we expected similarly slow responses to LH and LL trials in the Learning phase (as both were low-probability) but then faster responses to LH than LL in the Rewiring phase, indicating the acquisition of the more probable associations of Sequence B in this phase. Please note that all HH trials were Go during the Rewiring phase (for further details, see the "Supplementary methods" section in Supplementary Information). Consequently, learning scores involving LL trials were the primary measures of interest as these could be used to assess the effect of inhibitory control on rewiring (by contrasting learning scores calculated on those trials that were Go vs. No-go in the Testing phase).

cantly from zero in Period 2 ($p = 0.001$, Cohen's $d = 0.70$, $BF_{01} = 0.020$) and Period 3 ($p < 0.001$, Cohen's $d = 0.79$, $BF_{01} = 0.005$) of the Learning phase. In the Rewiring phase, learning scores started to slightly decrease (Period 1 vs. Period 2: $p = 0.050$, Cohen's $d = 0.37$, $BF_{01} = 0.840$; all other ps ≥ 0.178, Cohen's ds ≤ 0.25, BF_{01}s ≥ 2.210), reaching zero in Period 2 ($p = 0.726$, Cohen's $d = 0.06$, $BF_{01} = 4.926$), and then slightly bounced back in Period 3 ($p = 0.030$, Cohen's $d = 0.41$, $BF_{01} = 0.564$). The main effects were not significant (Phase: $F(1, 30) = 1.46$, $p = 0.237$, $\eta_p^2 = 0.046$; Period: $F(2, 60) = 1.74$, $p = 0.184$, $\eta_p^2 = 0.055$). Overall, participants successfully acquired the associations of Sequence A in the Learning phase and could at least partially unlearn this knowledge in the Rewiring phase.

Acquisition of new knowledge after structural change in the task. Learning of the new sequence occurred in the Rewiring phase (Fig. 3b, circled area): participants showed increasingly higher learning scores ('LL minus LH'), indicating faster responses to trials that were high-probability in Sequence B compared to low-probability ones (for raw RTs see Fig. S1a). Note that these associations were all low-probability in Sequence A; therefore, no learning was expected for them in the Learning phase ('LL minus LH'). The different time course of learning across the two phases was revealed by the significant Phase × Period interaction ($F(2, 60) = 3.89$, $p = 0.026$, $\eta_p^2 = 0.115$). Specifically, performance did not change significantly during the Learning phase (pairwise comparisons of periods: all ps ≥ 0.282, Cohen's ds ≤ 0.20, BF_{01}s ≥ 3.019) and did not differ significantly from zero (all ps > 0.339, Cohen's ds ≤ 0.17, BF_{01}s ≥ 3.390). In the Rewiring phase, learning scores increased from Period 1 to Period 3 ($p = 0.019$, Cohen's $d = 0.44$, $BF_{01} = 0.390$) and became greater than zero by the end of the task (Period 3: $p = 0.026$, Cohen's $d = 0.42$, $BF_{01} = 0.503$). The main effects were not significant (Phase: $F(1, 30) = 1.60$, $p = 0.216$, $\eta_p^2 = 0.051$; Period: $F(2, 60) = 0.20$, $p = 0.820$, $\eta_p^2 = 0.007$). In summary, these results confirm that participants acquired the associations of the new sequence after the structural change in the task. For a

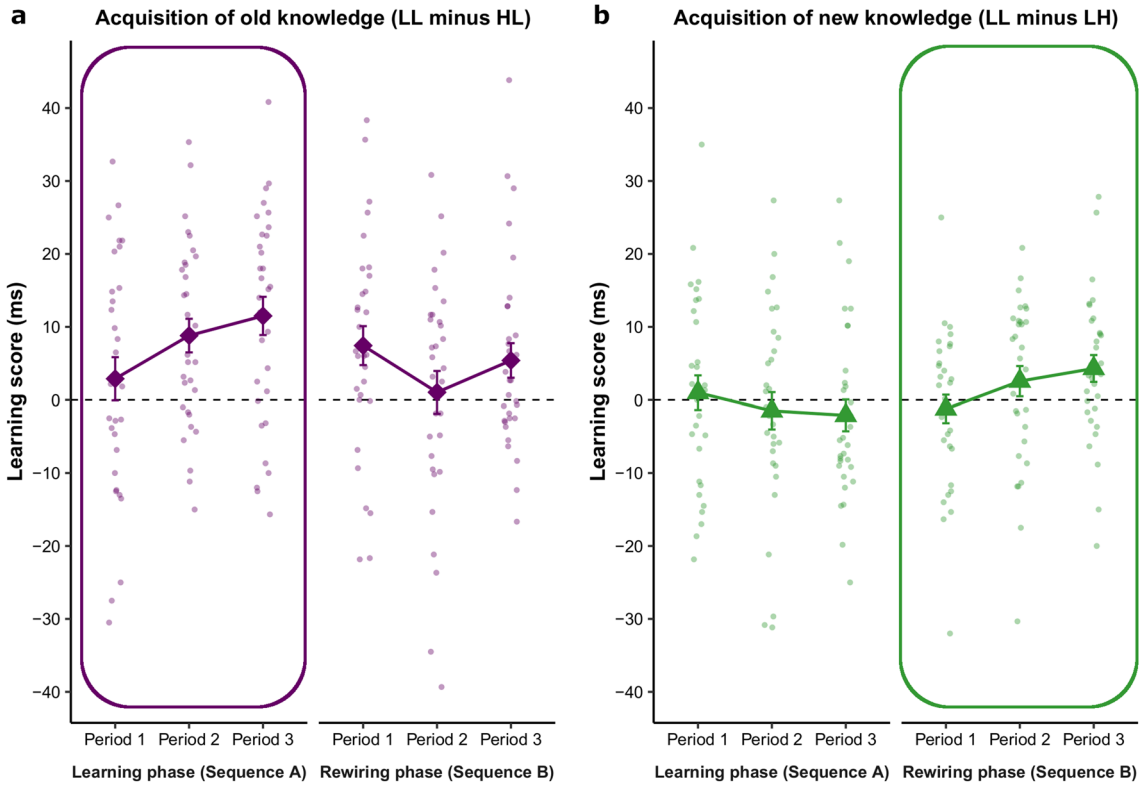

Figure 3. Learning trajectories of old and new knowledge in the learning and rewiring phases. The circled panels indicate the experimental phase in which higher learning scores were expected based on the probability of the trial types of comparison. For example, for the old knowledge ('LL minus HL' learning score), higher learning scores were expected in the Learning phase as trials with high vs. low triplet occurrence probability were contrasted here ('LL minus HL', underlined letters indicating probabilities of the current comparison; see also Fig. 2). (**a**) Participants successfully acquired the old knowledge (associations of Sequence A) in the Learning phase, indicated by gradually increasing learning scores. Then they at least partially unlearned this old knowledge in the Rewiring phase. (**b**) The new knowledge (associations of Sequence B) was gradually acquired in the Rewiring phase. (Since these associations were all low-probability in Sequence A, no learning was expected for them in the Learning phase). Please note that learning scores used in these analyses were calculated for Go trials only because no reaction times were collected for No-go trials in the Rewiring phase. Error bars represent Standard Error of the Mean (SEM).

further analysis on how the acquisition of new knowledge compares with the initial learning process, see the Supplementary Information.

How did the inhibition of responses during rewiring affect the old knowledge? In the Testing phase, we probed whether the old knowledge (using the 'LL minus HL' learning score) was expressed both in the old testing context (when the order of stimulus presentation followed Sequence A) and the new one (when stimulus presentation followed Sequence B; see also Fig. 1 for design). Knowledge on the previously Go and No-go trials was contrasted in both testing contexts. As expected, learning scores were significantly higher when tested on Sequence A than on Sequence B (main effect of Sequence: $F(1, 30) = 10.11$, $p = 0.003$, $\eta_p^2 = 0.252$), regardless of the Go/No-go manipulation. At the same time, they were significantly above zero in both contexts, indicating that the old knowledge was expressed not only in its original context (Sequence A; 'LL minus HL', $p < 0.001$, Cohen's $d = 1.22$, $BF_{01} = 1.845^{e-5}$) but also in the new one (Sequence B; 'LL minus HL', $p < 0.001$, Cohen's $d = 0.71$, $BF_{01} = 0.147$), where it was no longer relevant.

Crucially, the magnitude of learning scores depended both on the testing context (Sequence A vs. B) and whether responses were inhibited during rewiring (Go vs. No-go trials), as indicated by the significant Sequence × Inhibition interaction ($F(1, 30) = 11.81$, $p = 0.002$, $\eta_p^2 = 0.282$). When tested on Sequence A (Fig. 4a, circled area), learning scores were significantly above zero on Go and No-go trials ($p = 0.001$, Cohen's $d = 0.63$, $BF_{01} = 0.042$; $p < 0.001$, Cohen's $d = 1.25$, $BF_{01} = 6.508^{e-6}$, respectively) and somewhat greater for the latter ($p = 0.018$, Cohen's $d = 0.45$, $BF_{01} = 0.360$). This suggests that, instead of facilitating the unlearning process, inhibition potentially strengthened the expression of old knowledge in the old context. When tested on Sequence B (Fig. 4a, non-circled area), learning scores did not differ significantly on Go and No-go trials ($p = 0.500$, Cohen's $d = 0.12$, $BF_{01} = 4.210$). Importantly, participants performed significantly above zero on both (Go trials: $p = 0.004$, Cohen's $d = 0.55$, $BF_{01} = 0.112$; No-go trials: $p = 0.025$, Cohen's $d = 0.42$, $BF_{01} = 0.486$), again indicating that old knowledge was expressed even when it was not relevant, irrespective of whether responses were inhibited during rewiring.

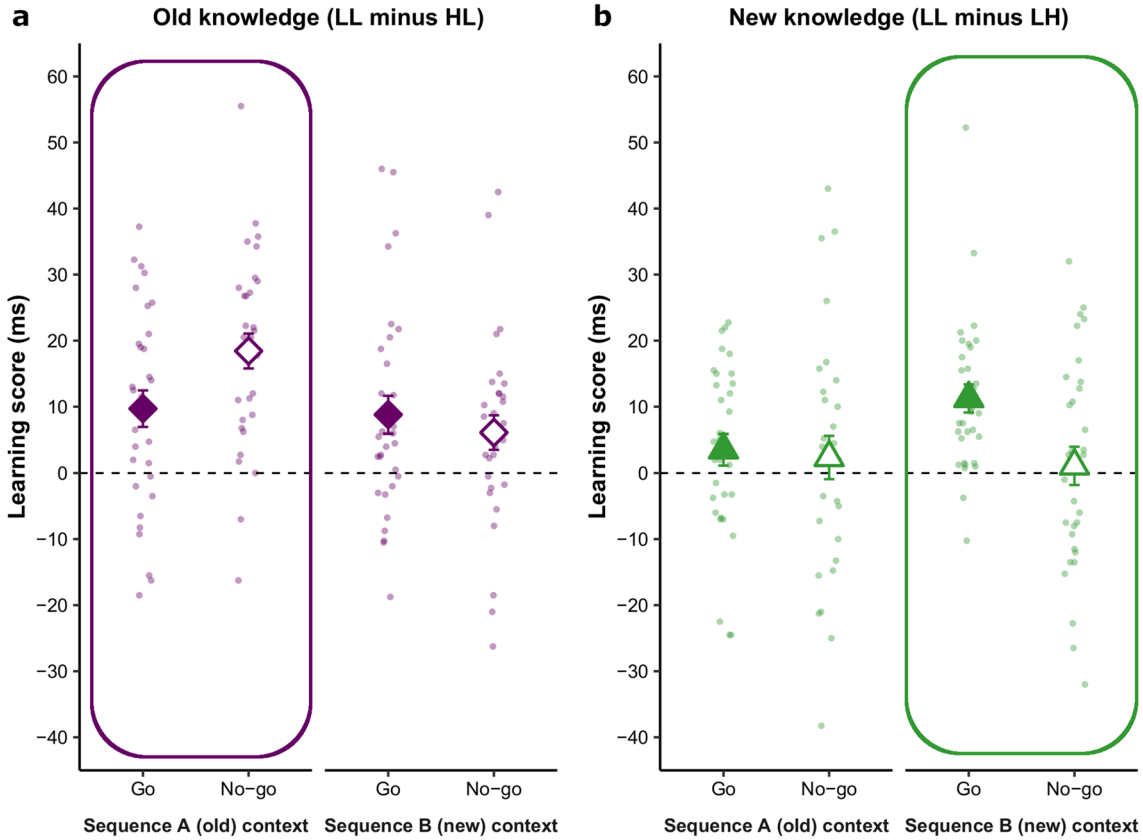

Figure 4. The effect of inhibitory control on old and new knowledge as revealed by performance in the Testing phase. The circled panels indicate the testing context (task version with Sequence A or B) in which higher learning scores were expected. For example, for the new knowledge ('LL minus LH' learning score), higher learning scores were expected in the new context (when stimulus presentation order followed Sequence B), since trials with high vs. low triplet occurrence probabilities were contrasted here ('LL minus LH', underlined letters indicating probabilities of the current comparison; see also Fig. 2). (**a**) Old knowledge. When tested on Sequence A (the original, old context), participants showed significant above-zero performance on Go and No-go trials, with significantly higher learning scores for the latter. This suggests that the old knowledge was present, and inhibiting responses during rewiring strengthened, instead of facilitated, its unlearning. When tested on Sequence B (the new context), participants exhibited similar, significantly above-zero learning scores on Go and No-go trials, suggesting that old knowledge was expressed even when it was not relevant, irrespective of whether responses were inhibited during rewiring. (**b**) New knowledge. When tested on Sequence B (the relevant, new context), participants showed significant above-zero learning scores only on Go trials and these learning scores differed significantly from those on No-go trials, indicating that new knowledge could be expressed only if responses were allowed to the relevant stimuli during rewiring. Thus, actively engaging in the new behavior-to-be-learned seemed essential for acquiring (and subsequently accessing) the new knowledge. When tested on Sequence A, participants' learning scores did not differ significantly from zero either on Go or No-go trials. This was expected since contrasted trials were all low-probability in Sequence A ('LL minus LH'). Error bars represent SEM.

From another perspective, learning scores on Go trials did not differ significantly across testing contexts ($p = 0.735$, Cohen's $d = 0.06$, $BF_{01} = 4.945$). In contrast, learning scores on No-go trials were significantly higher when tested on Sequence A than Sequence B ($p < 0.001$, Cohen's $d = 0.83$, $BF_{01} = 0.003$), suggesting that the detrimental effect of inhibition (boosting, instead of decreasing old knowledge) was greater in the old context than the new one. The main effect of Inhibition was not significant ($F(1, 30) = 0.83$, $p = 0.37$, $\eta_p^2 = 0.027$). Overall, these results highlight the persistence of old knowledge across testing contexts and suggest a detrimental effect of the inhibition of responses during rewiring.

How did the inhibition of responses during rewiring affect the new knowledge? In the Testing phase, new knowledge ('LL minus LH') was differentially expressed depending both on the testing context (Sequence A vs. B) and whether responses were inhibited during the Rewiring phase (Go vs. No-go trials), indicated by the significant Sequence × Inhibition interaction ($F(1, 30) = 4.20$, $p = 0.049$, $\eta_p^2 = 0.123$). When tested on Sequence A, learning scores did not differ significantly from zero either on Go or No-go trials ($p = 0.150$, Cohen's $d = 0.27$, $BF_{01} = 1.956$ and $p = 0.478$, Cohen's $d = 0.13$, $BF_{01} = 4.115$ respectively; Go vs. No-go: $p = 0.780$, Cohen's $d = 0.05$, $BF_{01} = 5.030$). This was expected because the contrasted trials were all low-probability in Sequence A

('LL minus LH'; Fig. 4b, non-circled area). When tested on Sequence B (the context relevant to new knowledge; 'LL minus LH', Fig. 4b, circled area), learning scores were significantly above zero on Go trials ($p < 0.001$, Cohen's $d = 0.95$, $BF_{01} = 5.084^{e-4}$) but not on No-go trials ($p = 0.710$, Cohen's $d = 0.07$, $BF_{01} = 4.889$). The difference between learning scores on Go vs. No-Go trials was significant ($p = 0.003$, Cohen's $d = 0.58$, $BF_{01} = 0.078$). This indicates that participants could successfully express new knowledge only if permitted to respond to the relevant stimuli during rewiring.

Conversely, although performance on No-go trials did not differ significantly across testing contexts ($p = 0.694$, Cohen's $d = 0.07$, $BF_{01} = 4.853$), performance on Go trials did: learning scores were significantly higher when tested on Sequence B vs. on Sequence A ($p = 0.009$, Cohen's $d = 0.50$, $BF_{01} = 0.201$). This suggests that newly acquired knowledge was successfully expressed only in its relevant context. The main effects were not significant (Sequence: $F(1, 30) = 2.56$, $p = 0.120$, $\eta_p^2 = 0.078$; Inhibition: $F(1, 30) = 3.74$, $p = 0.063$, $\eta_p^2 = 0.111$).

Overall, these findings indicate that participants successfully acquired the new knowledge on Go trials (for which responses were allowed during rewiring) and could express it in the appropriate context (i.e., when tested on Sequence B). At the same time, poorer performance on No-go trials suggests that *actively* engaging in the new behavior-to-be-learned may be essential for acquiring new associations and, consequently, for habit change.

Discussion

Changing habits is challenging[3], but as threats of environmental and health disasters rapidly increase across the world[1,2], it is more important than ever to find effective ways to succeed. To do so, it is vital that we gain a thorough understanding of how habits form and change. Previous research has extensively focused on non-human animals, reward-related behaviors, and clinical populations in humans, and characterized how simple stimulus–response(-reward) associations contribute to habit formation and change[16,17]. However, it is poorly understood how habit change occurs in healthy humans when more complex associations (i.e., when not only the current stimulus influences the response but a sequence of preceding stimuli) are learned and modified without explicit rewards. These features more closely resemble how habits form and change in daily life. Therefore, by probing how healthy human adults can form and rewire complex associations without explicit rewards, the present study can significantly contribute to our understanding of the key cognitive processes involved in habit change.

Using these features, we created a novel experimental design to test a widely held belief that inhibitory control could promote habit change[19,20]. In this design, we could test the acquisition of new habit-like behaviors and the simultaneous unlearning of old ones, and how inhibitory control affected both. Crucially, following the rewiring process, we probed both the old and new knowledge across original (old) and new testing contexts, and on those trials in which responses were or were not allowed previously, to reveal how inhibitory control affected the entire process of rewiring. We found that inhibiting responses had a detrimental effect on overcoming the old knowledge and establishing the new: old knowledge was retained and expressed not only in its original context but also in the new one; moreover, components of knowledge that were previously inhibited appeared to be even strengthened in the old context (Fig. 4a). New knowledge was expressed only in the new context and for those components to which responses were allowed (Fig. 4b), suggesting that actively engaging in the behavior-to-be-learned may be indispensable for successfully changing habit-like behaviors.

Our findings revealed the persistence of old knowledge in both the old and new contexts, irrespective of whether components were inhibited during rewiring. Recently, a new line of research on the competition between habitual and goal-directed responses following changes in stimulus–outcome[6] or stimulus–response[7] associations has revealed a similar persistence effect. Specifically, following extended training and under time pressure—shown to favor the expression of habit-like behaviors—reaction times increased for the goal-directed (desired) responses and participants committed a large proportion of habitual (undesired) errors. These findings highlight that habitual ("old") and goal-directed ("new") associations are in conflict during response selection, and, together with the present study, suggest that undesirable habit-like behaviors may exert their influence even if the desired behavior is ultimately executed (see previously not inhibited components of new knowledge exhibited successfully in their corresponding [new] context).

Inhibiting responses during rewiring shows some similarities with extinction learning, whereby the well-established, habit-like behavior (response) fades over time as the previously conditioned stimulus is repeatedly presented without any reinforcer[14,27,30,31]. Following extinction, relapse—reoccurrence of the extinct behavior/response—is often observed[17,32]. Our findings in the Testing phase show that relapse can occur not only when human participants encounter the original context e.g.[33,34] (akin to extinction learning studies) but also in the new context. This suggests that inhibiting unwanted behavior in everyday situations is ineffective in changing habits e.g.[35]. Importantly, as opposed to the typical settings in extinction studies, our results were observed without any explicit rewards being involved in either learning or rewiring, and alternative associations could be learned to replace the old ones (instead of just unlearning them). The persistence of old knowledge despite these characteristics suggests that extinction studies may underestimate the effect of suppressing old behaviors in habit change.

Our findings also suggest that inhibiting responses may even further strengthen cognitive representations underlying the original behavior we want to replace, resulting in a rebound effect. This is based on participants exhibiting higher learning scores on the previously inhibited components of old knowledge ('LL minus HL', No-go) compared to those that were not inhibited ('LL minus HL', Go), when tested in the old context (Sequence A). Note, however, that the effect size for this finding was slightly smaller (Cohen's $d = 0.45$) than the one used in the a priori calculations (a Cohen's d of 0.50; see the "Estimation of required sample size" section in the Supplementary Information) and, consequently, the post-hoc power appeared somewhat lower than expected (power = 0.68 for two-tailed comparisons, instead of the expected 0.80). Therefore, future studies are needed to replicate this rebound effect[6,7]. Beyond the persistence of old knowledge, our design could also reveal that

old and new knowledge coexisted in the new context (at least for those trials in which responses were allowed during rewiring). We observed this effect both in reaction time (RT) (reported in the main text) and response accuracy measures (see Supplementary Information). This finding could explain the competition that could occur between old and new behaviors during habit change, and thus serve as the cognitive basis for such competition[27]. To translate these findings to a real-life example, let us suppose that Mary has just moved to Country B. Here, recycling is much more prevalent than her previous residence in Country A, and she has therefore had to start dividing household waste into different bins depending on its material. In this case, the old behavior (throwing all household waste into the same bin) is expected to be gradually unlearned and replaced by the new behavior (dividing waste into separate bins). Despite the decision to change her behavior, it is possible that (i) when Mary re-visits Country A (old context) she reverts to not recycling (relapse of the old behavior), and (ii) even in Country B (new context), she might divide waste on some occasions but not on others (coexistence of old and new behaviors). Furthermore, Mary may, consciously or unconsciously, suppress some aspects of her habitual behavior of not dividing waste, which could exacerbate the above-described behavioral pattern. Since old and new behaviors coexist, and a continuous inhibition of the old behavior may be unsustainable over longer periods, our findings highlight that interventions using other approaches for habit change must be tested (for further discussion see[18,36,37]).

One might argue that our results are driven by an incomplete acquisition of the new knowledge as suggested by data from the Rewiring phase (see also the "How does acquisition of new knowledge compare with the initial learning process?" section in the Supplementary Information). However, some aspects of performance in the Testing phase suggest otherwise. Specifically, direct comparisons of old and new knowledge indicate that, of those trials on which responses were allowed during rewiring, participants could express old and new knowledge at a similar level, both when compared in their respective contexts (i.e., in Sequence A vs. Sequence B, respectively), as well as in the new (Sequence B) context (see "Is the level of the new knowledge comparable to that of the old knowledge in the Testing phase?" section in the Supplementary information). Since a 24-h delay period was included between the Rewiring and the Testing phases in our design, it is likely that consolidation (i.e., stabilization) of memory traces occurred in this period[23], facilitating the expression of newly acquired knowledge in the Testing phase. Future research should test how rewiring schedules with different durations of practice and different lengths of consolidation periods in-between[38,39] affect old and new knowledge across testing contexts.

In our experimental design, the duration of training for rewiring and the acquisition of old knowledge was the same. Recent studies showed that while we can acquire associative knowledge relatively quickly, updating it requires more extended practice[40,41]. Likewise, non-human animal studies of behavior change usually apply a non-fixed time window of training, lasting until the animal no longer exhibits signs of the original behavior[42,43]. Note, however, that this would be unfeasible in daily life as we may want to change behaviors that were developed and practiced over years or even decades. Consequently, in real-life examples of habit change, holding all other factors constant, we may expect an even weaker acquisition of new behavior and a stronger persistence of old behavior compared to what we observed in the current study. As the same amount of practice for new, preferred behaviors is unfeasible, new approaches need to be found and tested. Importantly, any such approach will need to track both the unlearning of old behavior and the acquisition of new behavior, as well as subsequently probe their coexistence—akin to the design of the current study.

What other factors should future research of habit change consider? While here, both the old and new knowledge were acquired incidentally (see also results of the free generation and triplet sorting tasks in the Supplementary Information), encouraging intentional processes during rewiring (e.g., providing explicit instructions on what aspects of behavior to change) may be beneficial, albeit potentially temporary[23]. This is consistent with the observation that aspects of learning may be initially accessible to consciousness, however, after extended practice, at least some components of the automatic, habitual behaviors are no longer consciously accessible[8,44].

The age when habits are acquired and then changed should also be considered. Although how people of different ages perform in habit change are poorly understood, research has shown that children, especially under the age of 12, are better at acquiring new complex associations underlying automatic behaviors, while older adults show significant difficulties in doing so, compared to young adults[45,46]. Our current study focused on young adults; investigating the same aspects of habit change in other age groups would be particularly important given the aging population across the world[47]. Since habit change involves not only unlearning old, unwanted behavior but also acquiring new, preferred behavior, we expect poorer performance and even stronger persistence of old behavior in older adults. Meanwhile, the childhood advantage in acquiring automatic behavior could be extensively utilized: ensuring that sustainable habits are learned in childhood could be key to succeeding in the global race for sustainability. Besides age, other characteristics of the sample should also be considered in the future: notably, the present study investigated educated young adults from the western world (often referred to as WEIRD people[48]), potentially limiting the generalizability of the present findings to a subgroup of the global population.

The present study applied an experimental design that was novel in several respects. First, we could track two key components of changing habit-like behaviors, that is, the acquisition of new knowledge and the simultaneous unlearning of old knowledge within the same task. Second, we investigated complex associations that could be acquired by responding to probability-based relationships between events of a stimulus stream, as opposed to more commonly used simple(r) stimulus–response associations in lab-based tasks. Third, we tested rewiring and the role of inhibitory control without explicit rewards or reinforcers, contrary to most human and non-human lab-based studies[27,43]. We considered this important as using rewards could evoke processes that are specifically related to the reward itself and would change the motivational/emotional aspects of habit change, possibly confounding the measurement of reward-independent learning processes underlying habit formation and change. These characteristics allowed us to more closely model how humans naturally develop habit-like behaviors[44,49,50] and test how inhibitory control affects key components of changing such behaviors. Nevertheless, as there are

numerous experimental tasks to test habit learning and change, all grasping (at least somewhat) different aspects of these processes (for more details see the "Behavioral and neural characteristics of habit learning across human and animal studies" section in the Supplementary information), further studies are needed to adapt our design to and test the role of inhibitory control in habit change with other tasks as well.

In conclusion, using a novel experimental design, we found that even though it is possible to acquire new habit-like behaviors, a parallel inhibition of the unwanted behavior may be maladaptive and may even strengthen the behavior we want to overcome. Thus, although inhibiting unwanted automatic behavior might be a natural reaction when attempting to replace unwanted, unsustainable habits with preferred, sustainable ones[19], employing inhibitory control during habit change seems to have no beneficial effect on this process. The design developed here could be used to test new approaches to habit change, thereby uncovering how they affect the cognitive basis of old and new habit-like behaviors, independent of reward effects, in healthy adults and other populations. This can help us develop new intervention techniques for habit change and thereby create more adequate policies, improving our odds of replacing unwanted automatic behaviors with preferred ones.

Methods

Participants. Thirty-three healthy undergraduate students participated in the experiment. They were attendees of a non-compulsory university course where course credits could be obtained by participating in scientific experiments and were randomly assigned to the present study. The sample size was determined based on previous studies using similar experimental tasks in within-subject designs[23,24] (for details, see the "Estimation of required sample size" section in Supplementary Information). Participants had normal or corrected-to-normal vision. None of them reported a history of any psychiatric or neurological condition, or substance use. One participant dropped out of the experiment due to technical errors during data collection. Another participant was excluded due to consistent outlier performance (± 2 SDs) on RT measures throughout the experiment. Therefore, 31 participants remained in the final sample (M_{Age} = 21.1 years, SD_{Age} = 2.15 years, $M_{Education}$ = 14.2 years, $SD_{Education}$ = 1.69 years, 29 females). They performed in the normal range on standard neuropsychological tests [Digit Span task[51,52]: M = 7.8, SD = 1.29; Counting Span task[53,54]: M = 3.7, SD = 0.70]. Prior to their inclusion in the study, participants provided informed consent to the procedure as approved by the Research Ethics Committee of the Eötvös Loránd University, Budapest, Hungary (Ref. no.: 2018/192). The study was conducted in accordance with the Declaration of Helsinki, and participants received course credits for taking part in the experiment.

Design. The experiment consisted of three phases, each separated by a 24-h (± 1 h) offline delay (Fig. 1). During the Learning phase (Day 1), participants performed a widely used and reliable[55] four-choice visuomotor reaction time task called Alternating Serial Reaction Time (ASRT) task[29,56], in which they acquired the associations of Sequence A. This is referred to as old knowledge throughout the paper. During the Rewiring phase (Day 2), a structural change was implemented in the task by introducing Sequence B. This change prompted the rewiring of old knowledge by acquiring associations of the new sequence. This is referred to as new knowledge. In this phase, participants were asked to suppress their responses on some trials (stimuli underlined with a red line during the task; No-go trials), while they were allowed to respond on other trials (Go trials). During the Testing phase (Day 3), participants completed a shorter version of the task, and performance was tested on both Sequence A and Sequence B in a counterbalanced order. In this phase, participants responded on all trials, including the ones that were No-go trials during the Rewiring phase. This enabled us to test how inhibitory control during rewiring affected the unlearning of old associations and the simultaneous acquisition of new associations. Throughout the experiment, participants were informed that they would participate in an experiment assessing reaction times and response accuracy changes over extended practice; thus, both learning and rewiring occurred incidentally[57]. This was chosen because in everyday situations many habits are developed incidentally[18,44]; note the current study aimed to test the role of inhibitory control on (un)learning processes and not the effect of incidental vs. intentional processes on rewiring, for that see[23]. For the detailed description of the ASRT task and the structural changes introduced in the Rewiring phase, see the "Supplementary methods" section in the Supplementary Information.

At the end of the Testing phase, a free generation task and a triplet sorting task were administered to probe whether participants acquired consciously accessible knowledge about the sequence and/or the probability structure of the task using recall- and recognition-based approaches, respectively. Since these tasks were not designed to contrast knowledge gained/rewired on Go vs. No-go trials, they served the sole purpose of testing whether any knowledge throughout the task became consciously accessible; the results are reported in the Supplementary Information for comparability across studies and to support future meta-analytic efforts.

Statistical analysis. *Learning phase and rewiring phase.* To track the trajectory of the acquisition and unlearning of old knowledge and the simultaneous acquisition of new knowledge, we analyzed the Go trials of these two phases. First, trials were categorized based on whether they were high- or low-probability in the Learning phase (according to Sequence A) and whether they were high- or low-probability subsequently in the Rewiring phase (according to Sequence B). This resulted in four trial types: HL, LH, HH and LL, in which the first letter denotes the probability in the Learning phase and the second letter denotes the probability of the same trial in the Rewiring phase (Fig. 2a; H—high-probability, L—low-probability). Second, data were grouped into three periods, each containing 15–15 ASRT blocks for both phases. Third, for each participant, period, and trial type, median RTs for correctly responded trials were computed.

Fourth, learning scores were computed as differences in response times on trials with changed (LH or HL) versus unchanged occurrence probabilities (LL or HH). Specifically, we expected that participants would become increasingly faster on HL trials during the Learning phase, as compared to the LL trials (for raw RT performance

see Fig. S1 in the Supplementary Information), resulting in increasingly higher learning scores ('LL minus HL', Fig. 3a) in this phase. This would indicate the acquisition of old knowledge[24,29]. Then, in the Rewiring phase, unlearning of this knowledge would be reflected in smaller/decreasing learning scores as in this case the initially high-probability trials became low-probability. Furthermore, we expected similarly slow responses to LH and LL trials in the Learning phase (reflected in near-zero learning scores) as here both were low-probability, and then faster responses to LH than LL in the Rewiring phase (reflected in increasingly higher/positive learning scores, 'LL minus LH', Fig. 3b), indicating the acquisition of new knowledge in this phase. The LL trials served as a baseline for these learning scores as they helped control for general practice effects, while no speed-up was expected on them due to probability-based learning as they were low-probability in both phases.

Finally, repeated-measures analyses of variance (ANOVAs) with Phase (Learning vs. Rewiring) and Period (Period 1, 2, 3) as within-subject factors were performed separately for the two learning scores (testing old and new knowledge).

Testing phase. In this phase, participants responded on all trials, including the ones that were No-go trials in the Rewiring phase. Therefore, both previously Go and No-go trials were analyzed here to test how inhibitory control during rewiring affected the old and new knowledge.

First, all trials were categorized as described above, resulting in four trial types (HL, LH, LL or HH). Second, data were grouped according to the tested sequence (Sequence A vs. Sequence B), both containing ten-ten ASRT blocks. Third, for each participant, each sequence, each trial type, and each response type (Go or No-go in the Rewiring phase), median RTs for correct trials were computed (for raw RTs see Fig. S1b in the Supplementary Information). Fourth, learning scores ('LL minus HL' and 'LL minus LH' for old and new knowledge, respectively) were computed as described above, separately for Sequence A and Sequence B, and separately for the previously Go vs. No-go trials. Finally, repeated-measures ANOVAs with the tested Sequence (Sequence A vs. Sequence B) and Inhibition (Go vs. No-go) as within-subject factors were performed separately for the two learning scores (testing old and new knowledge). This design enabled us to test (i) whether the old and new knowledge coexisted and was present even when it was irrelevant in a given context (e.g., positive learning score for the old knowledge when tested on Sequence B), and (ii) how inhibitory control during rewiring affected the old and new knowledge in these contexts (by contrasting performance on the previously Go vs. No-go trials, see Fig. 4).

In all analyses, Greenhouse–Geisser epsilon (ε) correction was used when necessary. Original df values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. For the significant interactions of the ANOVAs, pair-wise comparisons were performed using LSD post-hoc tests. We report Cohen's d as a measure of effect size for pair-wise comparisons. Additionally, inverse Bayes factors were computed using default JASP priors (JASP v.0.14.1.0[58]) to see if data provided evidence for the results obtained in the frequentist t-tests (anecdotal evidence for the null-hypothesis: $1 < BF_{01} < 3$, at least substantial evidence for the null-hypothesis: $BF_{01} > 3$; anecdotal evidence for the alternative hypothesis: $1 > BF_{01} > 1/3$, at least substantial evidence for the alternative hypothesis: $BF_{01} < 1/3$)[59]. To provide further contrasts across the learning scores of the old vs. new knowledge, additional analyses were performed where relevant (see Supplementary Information). All statistical tests were two-tailed. Figures were created using the *ggplot2* package[60].

Although RTs were the primary measures of interest in the current study, we performed similar analyses on the accuracy measures as well. These results are reported in the Supplementary Information, along with the results of the two additional tasks (free generation and triplet sorting tasks), which tested whether participants gained consciously accessible knowledge about the sequence and/or probability structure of the learning task.

Data availability

Data used for the analyses reported in this paper are available on the following online repository: https://osf.io/dt9b8/?view_only=5b6b8850ab8e412a9588a5842870346e.

Received: 5 December 2021; Accepted: 27 April 2022
Published online: 18 May 2022

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Acknowledgements
This research was supported by the National Brain Research Program (2017-1.2.1-NKP-2017-00002 to D.N.); Hungarian Scientific Research Fund (NKFIH OTKA PD 124148 to K.J., NKFIH OTKA K 128016 to D.N.), Janos Bolyai Research Fellowship of the Hungarian Academy of Sciences (to K.J.), the ÚNKP-20-3 New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund (to K.H.), and the IDEXLYON Fellowship of the University of Lyon as part of the Programme Investissements d'Avenir (ANR-16-IDEX-0005 to D.N.). The authors thank Anna Guttengéber, Ábel Gergely, Kirstóf Mikó, Péter Solymosi, Lilla Petrencsik and Dorottya Szily for their help in data collection. The authors also thank Jonathan L. Webb for his input on the language of the manuscript.

Author contributions
K.H. administered the project, supervised data collection, did formal data analysis, wrote the original version of the manuscript, and revised the manuscript. D.N. provided financial and theoretical support, supervised data analyses, and revised the manuscript. K.J. conceptualized and designed the study, created the experimental software, did formal data analysis, supervised data analyses, and revised the manuscript.

Funding
Open access funding provided by Eötvös Loránd University.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-022-11971-6.

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My doctoral research aimed to better understand the interplay between complex automatic behaviours and goal-directed behaviours during adaptation. Automatic behaviours were conceptualized using the procedural memory system, whereas goal-directed behaviours were modelled with components of the executive control system, namely attention, inhibition, and performance monitoring. I investigated this interplay without manipulating it, alongside the manipulation of the executive control system during acquisition, expression, and change of automatic behaviours. In this chapter, I will first summarise the main findings of the studies included in this dissertation. Second, I will discuss what these five studies showed about the procedural memory system, the executive control system, and their interaction. I will then cover the possible limitations of these studies and the questions the present dissertation opens.

IX. Main findings of the studies

In this chapter, I briefly sum up the main findings of each study and draw the most important conclusions about the relationship between automatic and goal-directed behaviours.

i. Study 1

Study 1 asked the question of how errors contribute to the acquisition and retrieval of an automatic behaviour in order to enhance task adaptation. More precisely, I investigated some aspects of performance monitoring by the most prominent ERP correlates of error processing, namely the Ne and the Pe in the cued version of the ASRT task. A common behavioural correlate of error-related adaptation, namely the PES effect was also assessed. Acquisition and retrieval were measured on the cued predictable events (pattern trials), while unpredictable events (improbable trials) served as a baseline.

At the behavioural level, we found that the order of the repeating pattern trials was rapidly acquired and performance on these trials increased subsequently. In contrast, no performance improvement was observed on the unpredictable events. It can be assumed that the former effects are grounded in the retrieval of the automatic behaviour developed based on the repeating pattern trials. That is, participants could (incidentally or intentionally) retrieve and use their knowledge about the repeating, predictable events to

achieve better performance in the task. It is important to note that acquisition and retrieval cannot be precisely and surely separated in the ASRT task, only assumed based on changes in the behavioural data.

The PES effect following errors decreased over time, similarly for both the retrieval and the baseline processes. As errors should imply the possibility of adaptively use them, it is conceivable that the decreasing post-error adaptation reflects the significance of errors becoming lower and lower. At the electrophysiological level, we found that the error negativity decreased over time, and it did so similarly across the retrieval and the baseline processes. This effect points towards the same direction as the decreasing PES: the significance of errors dropped in the task over time for both the retrieval of an automatic behaviour and the baseline process. Decreasing error significance is presumably grounded in the rapid adaptation to the task (Gehring et al., 1993; Hajcak et al., 2005). These findings together with a recent study showing successful acquisition of an automatic behaviour practically without errors (Vékony, Marossy, et al., 2020) may suggest that information derived from erring is not essential for automatic behaviour adaptation. The error positivity increased over time, and it did not differ between the retrieval and the baseline process. These effects suggest that error awareness enhanced as adaptation to the task progressed (Endrass et al., 2007; Nieuwenhuis et al., 2001), and this was not influenced by the retrieval of an automatic behaviour.

Overall, Study 1 showed that when an automatic behaviour can be retrieved to achieve better task performance, adaptation processes are present at the electrophysiological and behavioural levels. Nevertheless, these reflect general task adaptation instead of a retrieval-specific effect. Based on Study 1, automatic behaviours and aspects of performance monitoring do not interact during behaviour adaptation.

ii. Study 2

Study 2 aimed to answer the questions of when and to what degree we can adjust automatic behaviours when the environment becomes unpredictable without any noticeable change at the surface level. To this end, one group of participants first acquired an automatic behaviour (first part of the task), and then, this behaviour was challenged in a new environment (second part of the task). This new environment lacked the probability-based structure underlying the automatic behaviour and thus was unpredictable. As a control, another group of participants first practiced in the

unpredictable environment (first part of the task) and subsequently acquired the automatic behaviour based on the probability-based structure of the new environment (second part of the task). That is, in this group, the acquisition of an automatic behaviour took place following experience with the unpredictable environment. Crucially, the change in the underlying structure was always unsignalled (i.e., participants were not informed about it). So far, it has not been investigated how a complex automatic behaviour changes in such circumstances.

Prior to changing the underlying structure, procedural learning successfully took place in the group completing the predictable part first, whereas there was no learning in the group initially practicing the unpredictable part. After the unsignalled change in the environment, the following results emerged. On the one hand, in the group switching to the unpredictable part, the already established automatic behaviour persisted and was generalized to the unpredictable stimuli. Interestingly, this behaviour was then updated, and the automatic behaviour was no longer expressed by the end of the second part. However, this updating process took a longer time than initial acquisition. On the other hand, the group completing the unpredictable part first showed successful procedural learning in the subsequent predictable part. Moreover, their learning performance was comparable to the other group, despite already having been exposed to the unpredictable environment. That is, the predictable part influenced the subsequent behaviour on the unpredictable part, whereas the unpredictable part did not interfere with or influence in any way the performance on the subsequent predictable part (at least at the level of covert responses). These findings can also be interpreted as a proactive interference effect of a past memory trace, i.e., the previously acquired automatic behaviour interfering with the changed environmental structure (cf. Szegedi-Hallgató et al., 2017).

These findings showed that automatic, habit-like behaviours are persistent, and we tend to rely on them when facing an unpredictable environment. In other words, adaptation to a new environment can take place by relying only on our automatic behaviours. It is important to note, however, that in the present study, both parts of the task appeared similar at the surface level, thus participants faced a partly new environment that differed from the old one only in certain structural features. That is, it is presumable that maintaining the old behaviour in this situation may have been adaptive. On the other hand, this study also revealed that automatic behaviours can be updated and adjusted, if necessary, probably without the direct engagement of the executive control

system. Finally, the prolonged length of practice required for updating/adjusting the old behaviour provided further evidence for the persistent nature of our automatic, habit-like behaviours.

Overall, Study 2 showed that automatic behaviour adjustment and adaptation can successfully take place even if changes in the environment are hidden. However, it did not focus on and thus could not directly test the procedural memory vs. executive control system interplay during behaviour adaptation. Based on the results, it is unknown if and how participants spontaneously used their executive control system or relied solely on their procedural learning system when adjusting their behaviour.

iii. Study 3

The question of Study 3 was whether procedural learning remains intact when attention is divided between concurrent tasks and task goals. To answer this, a modified version of the cued ASRT task was used to induce the division of attention. As shown by Study 1, such a task is not difficult, in fact, the acquired knowledge can be intentionally retrieved to enhance performance. Therefore, a significant change was introduced to the task here; namely, instead of the commonly used self-paced design (e.g., Nemeth, Janacsek, & Fiser, 2013; Simor et al., 2019), we applied a fixed-paced and fast stimulus presentation. This modification aimed to prevent participants from intentionally learning and then retrieving the repeating predefined trials, dividing attention between their two goals in the task. A similarly fast and fixed-paced version of the original (un-cued) ASRT task was used as a control in a between-subject design. To assess whether divided attention differentially affected the retention of the acquired automatic behaviour, performance was retested after a 12-hour-long offline delay. The procedural learning of an automatic behaviour was assessed by comparing performance on the probable, but random and improbable random trials.

Indeed, participants completing the cued task version showed poor performance when asked to report the order of the repeating predefined trials, suggesting that the applied timing parameters prevented retrieval. Crucially, procedural learning did not differ between the groups. That is, despite the attention being divided, the acquisition of an automatic behaviour remained intact, in line with previous studies probing the effect of a secondary task on procedural learning and memory expression (Nemeth et al., 2011; Vékony, Török, et al., 2020). Even more so, performance following the offline delay was

also comparable across groups, showing that the automatic behaviour not only developed in a similar manner but was also retained just as successfully as without the divided attention manipulation.

To conclude, Study 3 showed that manipulating attention by dividing it between concurrent task goals does not interact with procedural learning or the offline retention of the acquired behaviour.

iv. Study 4

Study 4 investigated changing habit-like behaviours and the effect of response inhibition on this process. So far, it has been shown that i) automatic behaviours tend to "survive" rewiring procedures (Szegedi-Hallgató et al., 2019) and that ii) extinction, an experimental manipulation similar to a response inhibition manipulation, cannot successfully erase the old behaviour (Bouton 2000, 2004). In this study, the so-called old behaviour had to be changed according to a new environmental regularity (cf. Study 2 where the changed part consisted of unpredictable stimuli instead of a new regularity). Thus, not only the unlearning/forgetting/adjustment of the old behaviour but the development of a new behaviour was measured here. In addition, during habit change, response inhibition was engaged in the task to model the common urge of inhibiting unwanted behaviours.

In more details, participants practiced an extended version of the original ASRT task and acquired a habit-like behaviour on the first day. On the next day, this old behaviour was challenged: participants practiced a different but partially overlapping regularity and acquired a new automatic behaviour. Due to the overlapping nature of the new regularity, some parts of the old behaviour remained the same and were kept, while other parts had to be unlearned (or at least inhibited). On this day, a response inhibition manipulation was introduced to the task and participants had to suppress their responses in case of a warning sign (red line) presented together with the target stimulus, analogous to the standard Go/No-go paradigm. The occurrence of these stimuli was unpredictable, and a given proportion of all trial types had to be suppressed. Nevertheless, for those parts of the old behaviour that had to be unlearned, most responses had to be suppressed. Finally, on the third day, both the old and the new behaviour was probed without the response inhibition manipulation. In addition, both behaviours were probed in their

original context (i.e., the task contained the underlying regularity under which the behaviour was acquired) and in the opposite context, as well.

The following results were found in this study. First, the automatic behaviour was acquired during Day 1 (referred to as old behaviour). Next, the new behaviour was also acquired during Day 2, though learning scores were considerably lower than during the first day. This result could reflect the hindering effect of the response inhibition manipulation as well as the proactive interference effect deriving from the previously acquired behaviour (cf. Szegedi-Hallgató et al., 2017). Additionally, the old behaviour was somewhat unlearned in this phase. Interestingly, the sensitivity index, i.e., the difference between correct response rate and false alarm rate, revealed that response inhibition was supported by acquisition of the new behaviour. In other words, the sensitivity index was higher indicating high accuracy on the Go trials and low false alarm rate on the No-go trials on the predictable associations of Day 2. Nevertheless, it remains unclear in what ways learning could have supported response inhibition (e.g., increasing efficiency, decreasing demand). The results obtained during Day 3 showed that the old behaviour remained intact. In fact, it was expressed both in its original context as well as in the context of the new behaviour. Moreover, those units of the behaviour that had to be inhibited during rewiring were further strengthened. In contrast, the new behaviour was expressed only in its original context, and those behavioural units that were inhibited previously, could not be retained. Overall, a new habit-like behaviour was developed, but response inhibition had a detrimental effect on habit change. These findings complement a recent brain imaging study where evidence was found for implementing new habits being more feasible than diminishing old ones (Brevers et al., 2021).

Based on this study, there is a strong competitive relationship between procedural learning and the executive control system, or at least response inhibition during habit change. Accordingly, when we need to change a habit, it seems to be more adaptive to focus on acquiring and strengthening a new automatic behaviour instead of trying to inhibit the old one.

v. Supplementary Study

In this study, I aimed to investigate the relationship between acquisition of a complex automatic behaviour and interference suppression, the other core component of inhibition besides response inhibition. To do so, I introduced an Eriksen flanker-like

manipulation to the original (fully implicit) version of the ASRT task. Crucially, the flanker manipulation was unpredictable in the task. This design enabled us to directly test the interaction between procedural learning and interference suppression. According to the results, procedural learning successfully took place in the task and appeared to be similar across the different flanker congruency conditions (congruent, incongruent, neutral). The flanker congruency effect (difference between incongruent and congruent trials) was comparable across predictable (probable trials) and unpredictable events evidencing a similar level of interference, and surprisingly, generally decreased over time. A similar decrease effect in the Eriksen flanker task has not yet been reported, nevertheless, most studies use considerably shorter task versions. To the best of our knowledge, previous studies using flanked sequence learning tasks did not report a similar comparison of learning and flanker congruency effects (Li & Dupuis, 2008; Rüsseler et al., 2003).

An important aspect of behaviour adjustment in inhibitory control tasks is the congruency sequence effect, that is, a reduced flanker congruency effect following an incongruent trial (Egner, 2007, 2014). In this study, the CSE was found in the case of unpredictable events only (measured by both RTs and accuracy), whereas no such adaptation effect appeared on the predictable events. In fact, in the case of RTs, a reversed CSE was found for the predictable events; that is, the congruency effect was even higher following an incongruent trial than a congruent one.

Altogether, the basic findings of the Supplementary Study showed that procedural learning and interference suppression could take place independently in the task; however, some level of interaction could be present when uncertainty is high (cf. accuracy). Nevertheless, fine-tuned investigation of the CSE revealed a hampering effect between procedural learning and interference suppression. Particularly, when a task event can be predicted by the procedural learning system and previous trial incongruency induces conflict adaptation processes, this could result in a maladaptive overshoot and impaired performance (Bocanegra & Hommel, 2014), at least when measured by RTs. Meanwhile, the lack of CSE (expected or reversed) on probable trials measured by accuracy may suggest the opposite: when a task event can be predicted by the procedural learning system, there is no need for the executive control system to adjust to the varying level of conflict present in the task, saving mental resources. Future studies are needed to clarify these findings.

X. Individual differences in the procedural memory vs. executive control system interplay

Besides the different aspects and phases of procedural memory and the different subcomponents of the executive control system, individual differences may also influence the nature of these two systems' interplay, as recent computational modelling studies have highlighted. First, individual efficiency and potential of the procedural memory system were shown to be differently related to goal-directed performance (Park et al., 2020). While higher efficiency of learning in the ASRT task was associated with better inhibitory and shifting abilities, higher potential was associated with poorer inhibition and better spatial short-term memory. Second, when investigating the forgetting over an extremely extended period of time in the ASRT task, better updating and spatial short-term memory abilities were associated with better retention of procedural memory (Éltető et al., 2022).

Consequently, I conducted follow-up analyses for all five studies to gain some insight into if and how individual performances related to these two systems are associated. In Study 1-4, standard neuropsychological tests were assessed to obtain descriptive data on the samples' general cognitive functioning. These tests were now used for correlational analyses, separately for each study. More details about the analyses and the corresponding results can be found in Appendix V. To summarize, performance on neuropsychological tests appeared to be uncorrelated with performance on the ASRT task with one exception only. In Study 1, a significant association emerged between the percentage of perseverative errors in the Wisconsin Card Sorting Test (*shifting*) and the learning performance measured on the repeating cued pattern order (*procedural learning*) characterized by a strong negative correlation coefficient (Figure 3). In other words, better learning was associated with better shifting performance. It is conceivable that a good shifting capacity supports the intentional acquisition of the sequential information in the cued ASRT task. Unfortunately, the Wisconsin Card Sorting Test was not administered in Study 3 where a different version of the cued ASRT task was used, which could have provided further insight into this association.

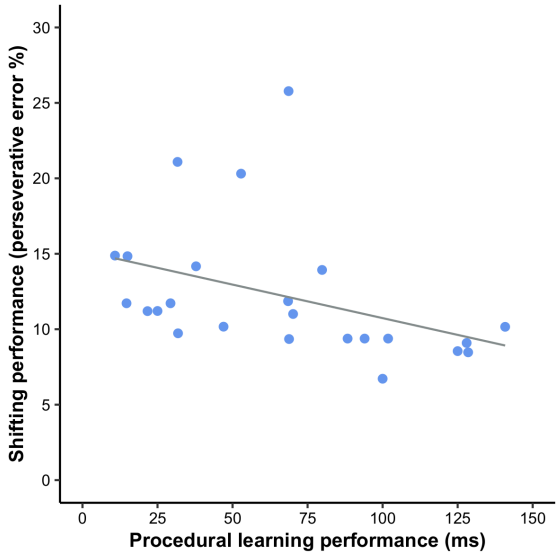

Figure 3. Significant correlation between procedural learning performance and shifting performance measured by the Wisconsin Card Sorting Test in Study 1. Please note that the negative correlation denotes a positive relationship here (i.e., better learning is associated with fewer perseverative errors, that is, with better shifting).

An important limitation of these analyses is that instead of probing the association of the two systems during their interplay, it can only reveal the relationship between performance measures assessed independently. Thus, based on these results, one cannot fully assume an independent relationship between procedural memory and the executive control system.

The design of the Supplementary Study enabled to overcome this limitation. To analyse the relationship between procedural learning and interference suppression, learning sores and flanker congruency effect scores were calculated. All neutral trials were excluded in this analysis. Learning scores were calculated as the difference in performance between high-probability pattern and low-probability random trials, separately for congruent and incongruent trials. For the congruency effect, the difference in performance between congruent and incongruent trials were calculated, separately for pattern and random trials. Correlations were tested using Pearson's *r* and, due to the smaller sample size, Kendall's τ-*B* as well. Additionally, I calculated BF_{01} values for all tests using default JASP priors (JASP Team, 2019). The results are summarised in Table 1.

Table 1. Association between procedural learning and interference suppression

$N = 36$			Pearson's		Kendall's		
			r	***p***	***τ-B***	***p***	**BF_{01}**
Learning effect Congruent	–	Flanker congruency effect Pattern	.145	.400	.065	.576	3.989
Learning effect Congruent	–	**Flanker congruency effect – Random**	**-.416**	**.012**	**-.283**	**.015**	**0.269#**
Learning effect Incongruent	–	Flanker congruency effect Pattern	-.220	.196	-.175	.134	1.559
Learning effect Incongruent	–	**Flanker congruency effect – Random**	**.489**	**.002**	**.322**	**.006**	**0.114#**

Note. Significant correlations are **bold-faced**. # Supported by the BF_{01} value on at least at a moderate level ($BF_{01} < 1/3$).

The analysis revealed significant associations between the flanker congruency effect measured on the low-probability random trials and the learning effect. This association, characterised by medium correlation coefficients, was reversed in direction on the congruent and incongruent trials, respectively (Figure 4). That is, the larger the flanker congruency effect (i.e., worse interference suppression), the smaller the learning effect on the congruent trials but the larger on the incongruent ones. These associations were further supported by the Bayesian approach.

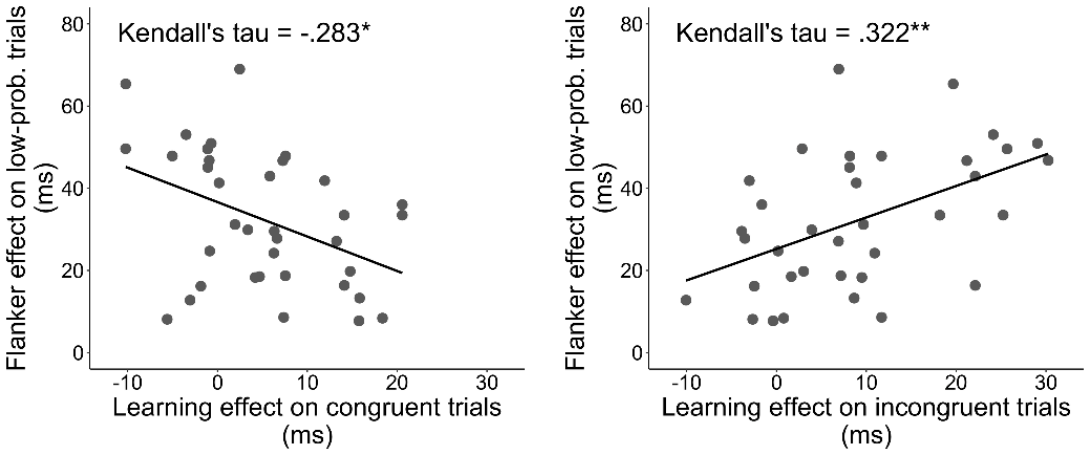

Figure 4. Significant correlations between procedural learning and the flanker congruency effect obtained in the Supplementary Study. A larger flanker congruency effect, that is, poorer interference suppression measured on the low-probability random trials was associated with poorer learning performance on the congruent trials, whereas the same flanker congruency effect was associated with better learning performance on the incongruent trials.

These findings of the Supplementary Study suggest that a possibly hampering relationship between procedural learning and interference suppression can emerge when these processes are simultaneously involved in the same task, especially when uncertainty and conflict are both high. On the other hand, when a trial is characterized by a lower level of conflict, this relationship is reversed. These findings require clarifications in the future.

To conclude the results obtained in these correlational analyses, individual procedural learning performance and executive control performance seem to be independent. In other words, when learning and executive control performance are assessed separately, there seems to be neither a trade-off nor a positive link between these abilities. However, when the two systems are involved in the same task simultaneously, their interplay can be revealed. Moreover, the nature of this interplay probably depends on the exact characteristics of the given task events.

XI. Independent or competitive relationship?

In this dissertation, I presented five studies that potentially combine the two major lines of research on the interplay of procedural memory and the executive control system. Here I focused on complex automatic behaviours, similarly to the competitive systems framework (Borragán et al., 2016; Nemeth, Janacsek, Polner, et al., 2013; Poldrack et al., 2001; Smalle et al., 2022), and modulated the executive control system in a similar way as in the associative learning account (Coomans et al., 2011; Deroost et al., 2012; Jiménez, Abrahamse, et al., 2020). Based on the findings presented in the dissertation, the nature of the interaction between automatic and goal-directed behaviours seems to be different according to which aspect of these behaviours is investigated.

Some results suggest an *independent* relationship: In Study 1, the retrieval of an automatic behaviour did not affect or interact with performance monitoring and adjustments following an error. In Study 3, acquisition, retention, and expression of an automatic behaviour were independent of attention being divided between two concurrent task goals. In the Supplementary Study, procedural learning took place irrespective of the level of interference in the task. Vice versa, interference suppression was independent of procedural learning in the task. Study 2 did not directly investigate this interplay. Yet, the update of a habit-like behaviour successfully took place that may or may not have included the spontaneous activation of the executive control system at least at some level (for further elaboration on this thought, see Subsection XIII.). These results are in line with some of the studies rooted in the associative learning account suggesting no interaction between procedural learning and goal-directed behaviours (Jiménez, Abrahamse, et al., 2020; Jiménez, Méndez, et al., 2020).

However, some results suggest an *interference* between automatic and goal-directed behaviours: In Study 4, response inhibition had a detrimental effect on both unlearning the old behaviour and acquiring the new one. That is, engaging response inhibition potentially hinders changing automatic behaviours. In the Supplementary Study, improved behaviour adjustment following a trial with high level of conflict was present only on uncertain and unpredictable events; whereas no such effect was present when a trial could be predicted based on probability. Even more so, a reversed effect was found suggesting a maladaptive overshoot of behaviour adaptation processes. That is, based on Study 4 and the Supplementary Study, there could have been an interaction between the procedural learning and the executive control systems which resulted in

interference and impaired performance. These findings are consistent with recent studies showing that engaging the executive control system interferes with procedural learning and memory expression (Prutean et al., 2022; Vaquero et al., 2020).

A converging pattern seems to emerge from these results. While an independent relationship was found when studying initial acquisition (Study 1, Study 3), competition/interference was revealed in more fragile situations (Study 4, Supplementary Study). Moreover, the nature of this interplay may vary across different phases of procedural learning processes and/or across the processes contributing to the executive control system. In other words, acquiring an entirely new automatic behaviour and then expressing it is simpler and less challenging than changing a habit when acquisition of the new habit is conflicted with the old one. Adapting to an uncertain and at the same time distracting environment is similarly complex and challenging, and adaptation based on the procedural memory system could be conflicted by adaptation based on the executive control system. The interference of these two systems appeared in such cases in the studies reported here. It is conceivable that instead of a black-and-white picture, the procedural memory vs. executive control system interplay shows different characteristics according to the combination of processes involved in it (e.g., acquisition is independent of attentional load vs. habit change is hindered by response inhibition). Accordingly, here I propose that our automatic and goal-directed behaviours may operate independently in situations where we can easily rely on the extraction of environmental patterns, in sort of an “autopilot” mode. However, when this extraction is conflicted, interference can emerge.

Another important implication of this dissertation is that whereas numerous studies using the ASRT task suggested a competitive relationship between procedural memory and goal-directed processes and/or the PFC, the studies presented here could not unequivocally support these findings. Instead, when the procedural memory system and the executive control system are *simultaneously involved* in a task, they do not seem to compete for mental resources or for selecting responses to be executed. Nevertheless, future studies are required to confirm or deny this proposal.

XII. The robust nature of procedural learning and memory

From another perspective, all these studies provided evidence for the robustness of procedural learning, retention of the acquired behaviour, and its expression even when the executive control system was heavily engaged in the task. Previous studies arrived at a similar conclusion when studying the procedural memory system in a wide range of experimental designs and clinical populations (e.g., Janacsek et al., 2018; Kiss et al., 2019; Kóbor et al., 2017; Nemeth et al., 2011; Obeid et al., 2016; Romano et al., 2010; Szegedi-Hallgató et al., 2017; Tóth-Fáber et al., 2021; Vékony, Török, et al., 2020). These studies are in line with the literature on increased reliance on habits under stress (Chaby et al., 2019; Tóth-Fáber et al., 2020; Wirz et al., 2018; Wood & Rünger, 2016). That is, even if the executive control system is permanently impaired or temporarily "switched off", the procedural memory system and our automatic behaviours can yet remain intact and contribute to behaviour adaptation.

Even though we often curse our automatic behaviours, especially bad habits or incorrect skills for being hard to alter, the robust, resistive, and inflexible nature of automatic behaviours is in fact adaptive. For example, we can reliably depend on these behaviours when the executive control system needs to engage with another task, like driving a car when trying to figure out the outline of a new, big city. Moreover, these findings may help us to develop new interventions, recovery, or coping techniques for those who suffer from neuropsychological impairment. The executive control system is impacted by various conditions, such as ADHD (Snyder et al., 2015), Tourette's syndrome (Yaniv et al., 2017), mild cognitive impairment (Brandt et al., 2009), or epilepsy (Elger et al., 2004). These populations could benefit from training methods that aim to compensate for their impacted abilities in the executive control system by improving or emphasizing automatic behaviour adaptation as an alternative.

XIII. Habit adjustment and habit change: Room for update as a goal-directed behaviour?

I have referred to changing or adjusting habit-like behaviours as "updating" them. Updating, however, is another auxiliary component of the executive control system (Bari & Robbins, 2013; Miyake & Friedman, 2012), which is responsible for updating task goals and relevant information when a new plan is needed for successful goal-directed

actions. It is presumable and in no ways neglectable that during habit adjustment/change, participants may have engaged their executive control system *spontaneously*. In more detail, when their old automatic behaviour was challenged by structural changes in the underlying sequence (from predictable to unpredictable environment in Study 2 and from an old structure to a partially new structure in Study 4), not only this behaviour was updated by the new incoming information but also the related action plans and goals. However, the studies included in the dissertation cannot confirm or deny this speculation as overt responses cannot reveal the underlying processes leading to updating habits (for further details see Subsection XIV. on p. 89).

XIV. From the viewpoint of the executive control system

Although the present dissertation put more emphasis on the understanding of the procedural memory system, the findings can be discussed from the direction of the executive control system, as well. In Study 1, error processing took place similarly across the repeating cued patten trials and the (uncued) random ones, suggesting that error processing did not specifically benefit from learning the sequential order in the ASRT task. It is inconclusive, nevertheless, whether the observed decrease in error significance and increase in error awareness were grounded in general task adaptation rather than in procedural learning. In Study 4, response inhibition hindered the change of habit-like behaviours; however, response inhibition seemed to be supported by the procedural memory system according to the results from Day 2 (for more details see the Supplementary information of Study 4; Verbruggen & Logan, 2008a). Finally, in the Supplementary Study, a general decrease was observed for the flanker congruency effect which might have been grounded in the support of procedural learning (Deroost et al., 2012; Jiménez, Abrahamse, et al., 2020; Koch, 2007). To conclude, approaching the procedural memory vs. executive control system interplay from the viewpoint of the latter highlighted that for revealing the full picture, both directions of the interplay should be considered.

XV. Graphical overview of the main findings and conclusions

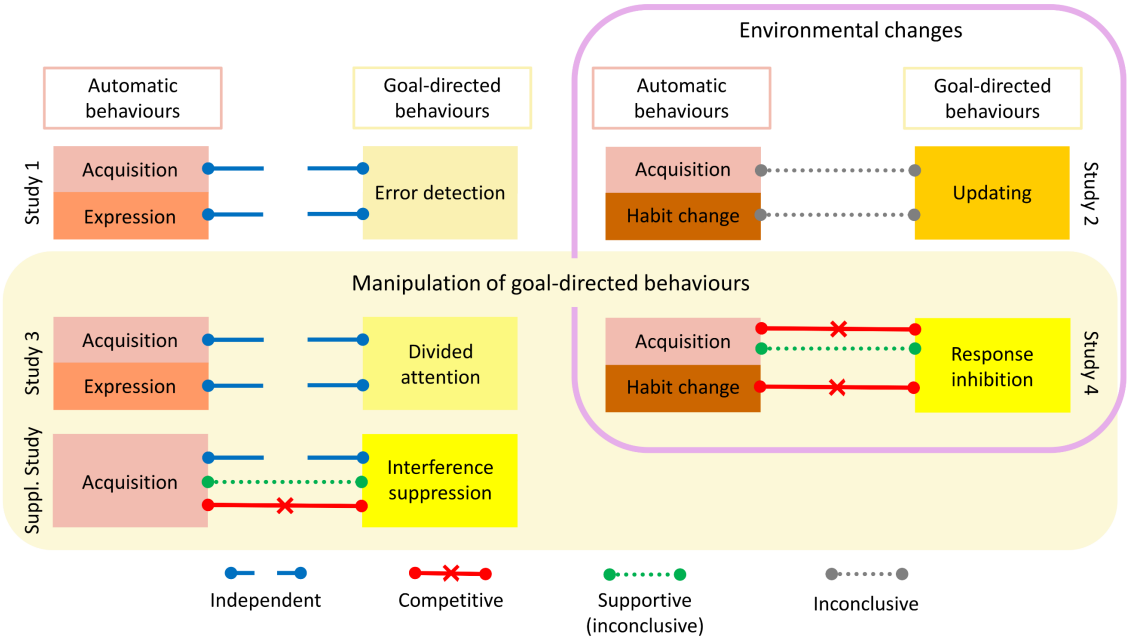

Figure 5. Summary of studies and main findings. Study 1 and Study 2 investigated the procedural memory vs. executive control system interplay during behaviour adaptation without manipulating either. Study 3, Study 4, and the Supplementary Study involved the experimental manipulation of the executive control system (yellow background shading). Study 1, Study 3, and the Supplementary Study focused on acquisition and expression, whereas Study 2 and Study 4 investigated habit adjustment and habit change grounded in environmental changes (purple framing). I found evidence for independent (blue), interfering (red), and supportive (green) relationships, with the latter being inconclusive (dotted). Grey dotted lines indicate relationships whose natures are currently unknown.

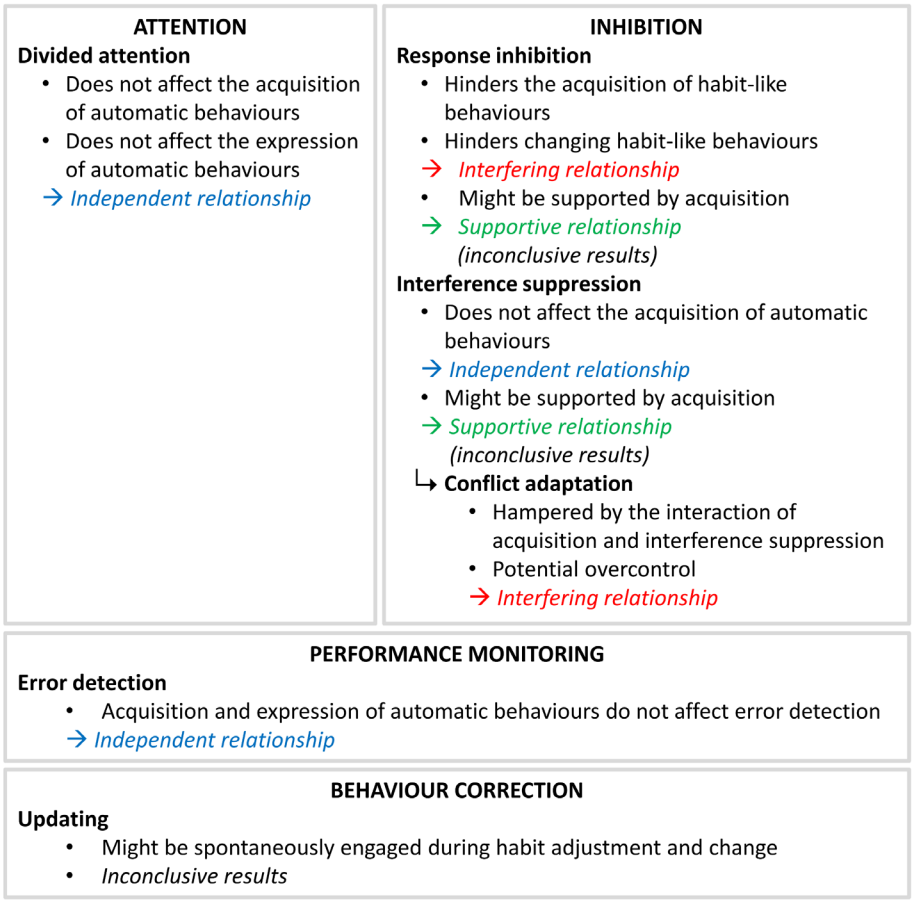

Table 2. Summary of conclusions. According to the findings presented in the dissertation, the interplay of automatic and goal-directed behaviours during adaptation is not uniform but depends on the (sub)processes and aspects of the two systems involved in the task.

XVI. Limitations and future remarks

The present dissertation is not without limitations. In this subsection, I will discuss these limitations and provide possible solutions for overcoming them. Next, I will cover the potential future directions and the questions opened by my doctoral research.

First, in my dissertation, I presented various evidence for an independent relationship between the procedural memory system and the executive control system. These statistically negative findings could have been the result of low sample size and power; however, I would like to argue that this is not the case in the presented studies. On the one hand, in Study 1-3 and the Supplementary Study, we followed best practices based on previously published studies using the ASRT task and aimed for at least around 25 participants per groups. In Study 4, detailed a priori sample size calculations were

conducted using previously collected data from a similar task design. On the other hand, effect sizes of the significant findings were at least moderate but most often strong, suggesting sufficient power in all five studies. Nevertheless, I conducted "a posteriori" sample size calculations using G*Power 3.1.9.6 (Faul et al., 2007) with an *f* effect size of 0.3 (typical in ASRT studies) and a power of 0.8 (moderate effect) and found that a N = 25 sample is indeed sufficient to show a significant main effect of a two-level variable (e.g., trial type in the present case). In addition, I conducted post-hoc Bayesian analyses for the insignificant findings where the original article did not include these. None of the originally published frequentist results were in contradiction by the Bayesian approach, further suggesting that the present null-results ("independent relationship") are not due to the lack of power.

Second, another noteworthy limitation of the dissertation is that although several aspects, phases, and subcomponents of the two systems were targeted in the five studies, their combinations were not fully comprehensive. For example, it remained unclear whether response inhibition hinders the original acquisition of a fully new automatic behaviour as well, or if the division of attention would interact with the adjustment of habit-like behaviours. I also neglected the processes responsible for correcting the suboptimal behaviour: (goal-directed) updating, shifting, and (plan) selection. Future studies should manipulate these processes during procedural learning, memory retention and expression, and habit adjustment/change to get a fuller picture about the nature of the procedural memory vs. executive control system interplay in behaviour adaptation. Furthermore, while some studies experimentally manipulated the engagement of the executive control system, none manipulated the procedural memory system. For instance, the complexity level of the underlying structure that can be extracted and acquired could be simplified or complicated, highlighted, made partially explicit, or mislead by certain cues, thereby modulating the engagement of the procedural memory system. On a related note, as behavioural, neural, and clinical findings regarding the procedural memory system often appear to be task-, modality-, and domain-dependent (Bogaerts et al., 2022; Conway, 2020; Frost et al., 2019; Schapiro & Turk-Browne, 2015), the present questions and designs should be expanded to different tasks, such as embedded pattern tasks or artificial grammar learning tasks.

Finally, by focusing only on behavioural indices, crucial aspects of this interplay could remain hidden. ERPs are a powerful tool to reveal the temporal unfolding of

cognitive processes involved in the task from stimulus processing to response execution and the formation of expectations about the upcoming stimulus. Therefore, future studies should adapt the present designs for the study of ERPs and investigate how these steps take place and vary according to which processes and at what level are involved in the task. Non-invasive brain stimulation methods offer the possibility of altering the activity of certain brain regions and neural networks and draw causal links between the targeted structures and the behaviour. Thus, these methods could help us unveil how and which regions and networks contribute to behaviour adaptation based on the procedural memory and the executive control systems and their interplay. Additionally, studying clinical populations with impaired behaviour adaptation processes could get us closer to fully understand its behavioural and neural background. Besides the populations with impaired goal-directed behaviours listed in a previous subsection (p. 87), patients with impairments of the basal ganglia, like in Huntington's disease and in Wilson's disease (Rosenblatt & Leroi, 2000), or with impairments of the cerebellum, like in Spinocerebellar ataxia (Koeppen, 2005), should be examined.

XVII. Conclusions

The five studies included in this dissertation aimed to gain insights into the interaction of automatic and goal-directed behaviours during adaptation. I presented various evidence that our automatic behaviours are highly robust and independent of the operation of the executive control system. Importantly, however, when more fragile aspects of procedural learning and memory were inspected, such as the challenge of habit change or behaviour adjustment during uncertain events, competition/interference between the two systems was revealed, which was further strengthened by the analyses of individual differences in procedural memory performance and executive control performance. By taking forward the study designs and focusing on the issues raised in this dissertation, we could get closer to unravel the interplay of automatic and goal-directed behaviours, and thereby develop methods to improve behaviour adaptation in our everyday life.

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APPENDIX I: SUPPLEMENTARY STUDY

Supplementary Study: Manipulation of inhibitory control does not influence procedural learning

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Related publication:

- **Horváth K.,** Kardos, Z., Takács, Á., Janacsek, K., Nemeth, D., & Kóbor, A. (2021). Manipulation of cognitive control does not influence statistical learning: Evidence from a probabilistic sequence learning task combined with the Eriksen flanker paradigm. *ESCAN 2021: Conference of the European Society for Cognitive and Affective Neuroscience.* 23-26. July, Budapest, Hungary. *Online poster presentation.*

Background

The interplay of automatic and goal-directed behaviors is often studied in combined paradigms where stimulus presentation is determined by a predefined, repeating structure and the surface level contains interfering stimuli creating conflict in the task. Previous studies, however, revealed mixed results: some studies proposed a supportive relationship (Coomans et al., 2011; Deroost et al., 2012; Deroost & Soetens, 2006; Koch, 2007) and the necessity of goal-directed control for the successful expression of automatic behaviors (Thompson et al., 2014), while others argue for the independence of these processes (Jiménez, Abrahamse, et al., 2020; Jiménez, Méndez, et al., 2020). Importantly, these studies exclusively used simple deterministic sequences which cannot be well-translated to our everyday automatic behaviors. From another line of research, evidence for competition/interference between complex automatic behaviors and goal-directed behaviors has emerged (Ambrus et al., 2020; Nemeth et al., 2010, 2013; Poldrack & Packard, 2003; Smalle et al., 2022; Virag et al., 2015). Nevertheless, these studies disregarded the direct manipulation of goal-directed behaviors and applied solely correlational or interventional designs instead of combined paradigms.

In the present study, we aimed to overcome the shortcomings of these studies by creating a new experimental design: automatic behaviors were modelled via a probabilistic sequence learning task and goal-directed behaviors were modeled via an interference

suppression paradigm. More precisely, the Alternating Serial Reaction Time (ASRT) task (Howard & Howard, 1997; Kóbor et al., 2019) was combined with the Eriksen flanker task (Eriksen & Eriksen, 1974) in a way that the underlying sequence did not predict/correlate with the distractor stimuli (for more details see the Methods section).

Besides examining how procedural learning and interference suppression take place in the task, additional behavior adjustment effects can be identified and studied in similar task designs. The most prominent measure of conflict-driven adjustment processes is the congruency sequence effect (CSE) or Gratton effect. The CSE refers to the phenomenon that interference suppression (so-called congruency effect in the Eriksen flanker task) is less demanding (i.e., the congruency effect is reduced) following an incongruent trial than a congruent one (Egner, 2007, 2014; Schmidt, 2019). Measuring CSE in the present task enabled us to reveal the otherwise hidden aspects of the interplay between procedural learning and interference suppression.

Our results showed that i) procedural learning successfully took place in the task despite the flanker manipulation, ii) the distracting effect of the flankers was evident, thus interference suppression had to be involved in the task, iii) these processes seemed to be operating independently. However, when examining the CSE in the present task, a hampering relationship between procedural learning and interference suppression possibly emerged. A more detailed explanation and discussion of the present findings can be found at the end of each subsection of the Results section.

Methods

Participants

Forty-one healthy young adults participated in the experiment. Two of them were excluded for not meeting the recruitment criteria. Two more participants were excluded for technical errors. Thus, 36 participants remained in the final sample. All of them had normal or corrected-to-normal vision and none of them reported a history of any psychiatric and/or neurological condition and substance use (26 females and 10 males, M_{Age} = 22.4 years, SD_{Age} = 2.91 years, $M_{\text{Education}}$ = 14.9 years, $SD_{\text{Education}}$ = 1.89 years). Prior to their inclusion in the study, participants provided informed consent to the procedure as approved by the research ethics committee of the United Ethical Review Committee for Research in Psychology (EPKEB) in Hungary. The

study was conducted in accordance with the Declaration of Helsinki and participants received course credits or vouchers (equivalent to a payment of ca. 5.5 euros) for taking part in the experiment.

Task and procedure

The experiment consisted of one session. Participants performed a four-choice visuomotor reaction time task. To create a sequential flanker task, we combined the Eriksen flanker task (Eriksen & Eriksen, 1974)—a task assessing interference suppression—and the Alternating Serial Reaction Time task (Howard & Howard, 1997; Kóbor et al., 2019)—an implicit procedural learning task. This design enabled us to test how these two processes operate and interact when simultaneously involved in the task.

In this task, a centrally presented arrow target stimulus appeared together with four flanker stimuli—two on the left and two on the right (Figure 1). Four buttons of a response pad (Cedrus RB-540, Cedrus Corporation, San Pedro, CA) corresponded to the four spatial directions. Participants were asked to press the button corresponding to the target stimulus (left = left thumb, up = left index finger, right = right index finger, down = right thumb) when the stimuli appeared on the screen as fast and as accurately as they could. In 37.5% of trials, the direction of the flanker stimuli was congruent with the direction of the target stimulus (congruent condition). In 37.5% of trials, the flanker stimuli pointed to the opposite direction as the target stimulus (incongruent condition). In the remaining 25%, the flanker stimuli had no spatial properties (rectangular shapes, neutral condition). Participants were instructed to ignore the flanker stimuli.

Unbeknownst to the participants, the presentation of target stimuli followed an alternating regularity. In this regularity, predetermined pattern (P) trials alternated with randomly chosen ones (e.g., 2 – r – 3 – r – 4 – r – 1 – r, where numbers denote the four predetermined directions [1 = left, 2 = up, 3 = down, 4 = right], and *r*s denote the randomly chosen directions out of the possible four). Due to this alternating regularity, some runs of three consecutive trials (triplets) occurred with a greater probability than others. In the example above, 2 – x – 3, 3 – x – 4, 4 – x – 1, and 1 – x – 2 (where x denotes to the middle element of the triplet) were more probable, as these were presented in every sequence repetition and also by chance. Meanwhile, for instance, 2 – x – 1, 3 – x – 2, 4 – x – 3, and 1 – x – 4 occurred less

probably as these triplets could only be formed by chance. We refer to the former category as high-probability triplets (62.5% of all trials), whereas low-probability triplet denotes the latter category (37.5% of all triplets). For all triplets, the third element (*n*) of a triplet was predictable by the first element (*n*-2) of that triplet with either high or low probability, while the middle element (*n*-1) did not have a predictive value. Triplets were identified using a moving window throughout the stimulus stream; thus, each trial was categorized as the last element of a high- or low-probability triplet; then, the same trial served as the middle and the first element for the categorization of the following triplets (Figure 1). Importantly, those random trials that were the third elements of a high-probability triplet (random high-probability trials) could be considered as "accidentally-regular" and seem to be characterized by unique response biases (Kóbor et al., 2018, 2019; Szegedi-Hallgató et al., 2019). Consequently, all random high-probability trials were excluded from the analysis (Horváth et al., 2021; Kóbor et al., 2021).

The task was organized into blocks, each consisting of 85 trials. In the first five trials, randomly chosen arrows were presented and served as a warm-up; this was followed by ten repetitions of the eight-element alternating sequence. All stimuli were presented as the combination of a central target stimulus and four flanker stimuli (two on the left, two on the right). The flanker congruency of the five warm-up trials were randomly selected, whereas the congruency of each trial of the repeating sequence was predetermined based on but not predicted by the ASRT sequence. In more details, flanker congruency was defined for the last trials of every unique triplet (64 altogether), and for all occurrences of a given unique triplet, the last trials had the same flanker congruency. 37.5-37.5% of both high-probability and low-probability triplets were assigned into the congruent and incongruent categories, while the remaining 25-25% were assigned into the neutral category.

Stimuli—target and flanker—were presented centrally on the screen for 200 ms. Then, a blank screen was presented until a response was provided but no longer than 500 ms. If participants responded during stimuli presentation, the stimuli disappeared. Following, another blank screen was presented for 700 ms (response-to-stimulus interval, RSI); then, the next stimuli appeared. In the case of an incorrect response, 500 ms after incorrect response onset, a black "X" was presented for another 500 ms. In the case of no response within the given time window, an "!" was presented for 500 ms. The experiment consisted of 30 blocks altogether, following a two-block practice where all stimuli appeared in a random order (Kóbor et al., 2019). A short self-paced break was administered before each block started. After completion

of the task, a short post-task questionnaire was assessed. Participants were asked to report anything special observed and/or any regularity discovered in the task. None of them reported any regularity possibly linked to the ASRT sequence.

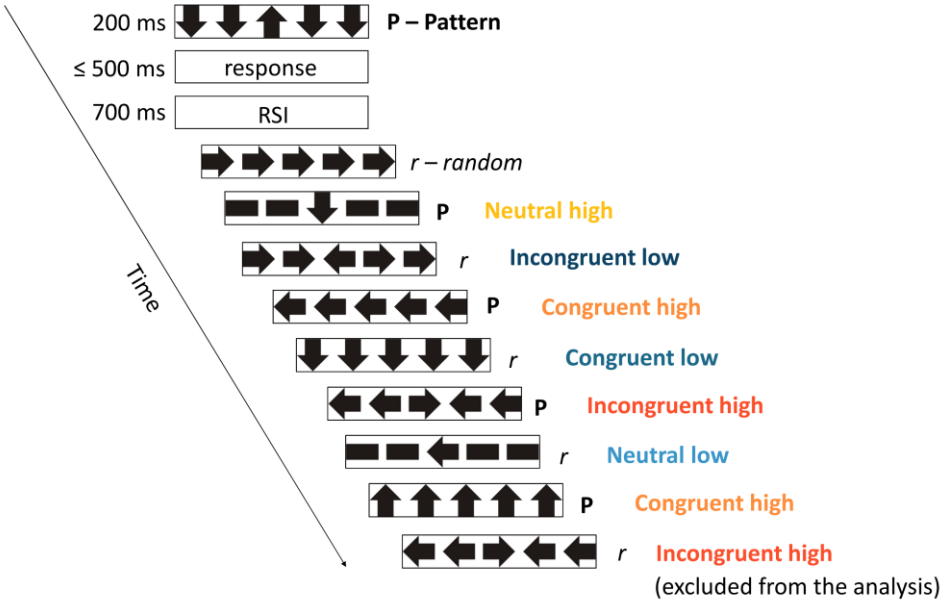

Figure 1. Design of the task. Stimuli (target and flanker) were presented for 200 ms, then, participants had a maximum of 500 ms to provide a response. Following a blank screen presented for 700 ms (RSI), the next stimuli appeared on the screen. Trial congruency was either congruent (37.5% of all trials), incongruent (37.5%) or neutral (25%), and was defined based on but not predicted by the ASRT sequence.

Statistical analysis

Trial types were determined by the combination of probability (high/low) and congruency (congruent/incongruent/neutral). First, data were grouped into three equal time bins (periods), each including ten task blocks to track the trajectory of performance (for a similar approach, see Horváth et al., 2021). Second, median RTs for correctly responded trials and mean response accuracy were calculated separately for all trial types in each period. Finally, the RT and accuracy data calculated at the participant level were submitted into separate Probability (2) x Congruency (3) x Time (3) repeated-measures analyses of variance (ANOVAs). Procedural learning, i.e., the acquisition of probability-based associations, was measured as the difference in performance between (pattern) high-probability and low-probability trials (Kóbor et al.,

2021). The congruency effect was measured as the difference in performance between congruent and incongruent trials (Botvinick et al., 1999; Egner, 2007; Gratton et al., 1992).

To probe whether a conflict driven-adjustment effect, namely, the congruency sequence effect (CSE; Egner, 2007), was present in the task, congruency of the previous trial was additionally considered. Neutral trials and trials following a neutral trial were excluded in this analysis. Thus, eight trial types were distinguished based on probability (high/low), current trial congruency (congruent/incongruent), and previous trial congruency (congruent/incongruent). The calculated RT and accuracy data of these trial types were then submitted into separate Probability (2) x Current (2) x Previous (2) repeated-measures ANOVAs.

Greenhouse-Geisser epsilon (ε) correction was used when necessary. Original df values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. LSD correction was used for pair-wise comparisons to correct for Type I error. All tests were two-tailed. All figures were created using the *ggplot2* (Wickham, 2016) package.

Results

Does interference suppression influence the extraction and acquisition of probability-based associations?

Reaction time – Learning was successful (main effect of Probability, $F(1, 35) = 58.63$, $p < .001$, $\eta_p^2 = .626$) and a strong congruency effect was found (main effect of Congruency, $F(2, 70) = 144.21$, $\varepsilon = .716$, $p < .001$, $\eta_p^2 = .805$), which was decreasing over time (Congruency * Time interaction, $F(4, 140) = 17.62$, $\varepsilon = .766$, $p < .001$, $\eta_p^2 = .335$; Figure 2). Importantly, the learning effect and the congruency effect seemed not to influence one another as shown by the non-significant Probability * Congruency interaction ($F(2, 70) = 1.05$, $p = .357$, $\eta_p^2 = .029$). General performance—irrespective of trial type—improved over time (main effect of Time, $F(2, 70) = 48.59$, $p < .001$, $\eta_p^2 = .581$). The Probability * Time interaction and the triple interaction did not reach significance ($F(2, 70) = 0.63$, $p = .537$, $\eta_p^2 = .018$; $F(4, 140) = 1.16$, $p = .332$, $\eta_p^2 = .032$, respectively). Overall, despite the task having combined procedural learning and interference suppression manipulations, we observed statistically strong learning effect and congruency effect. These two effects seemed to be present independently. Interestingly, the flanker congruency effect decreased as the task progressed suggesting adaptation to the

interfering stimuli (Figure 2). To the best of our knowledge, no such effect has been reported so far, raising the possibility that procedural learning supported interference suppression over time. Nevertheless, future studies are needed to clarify this effect as typical flanker tasks contain far less trials than the present one.

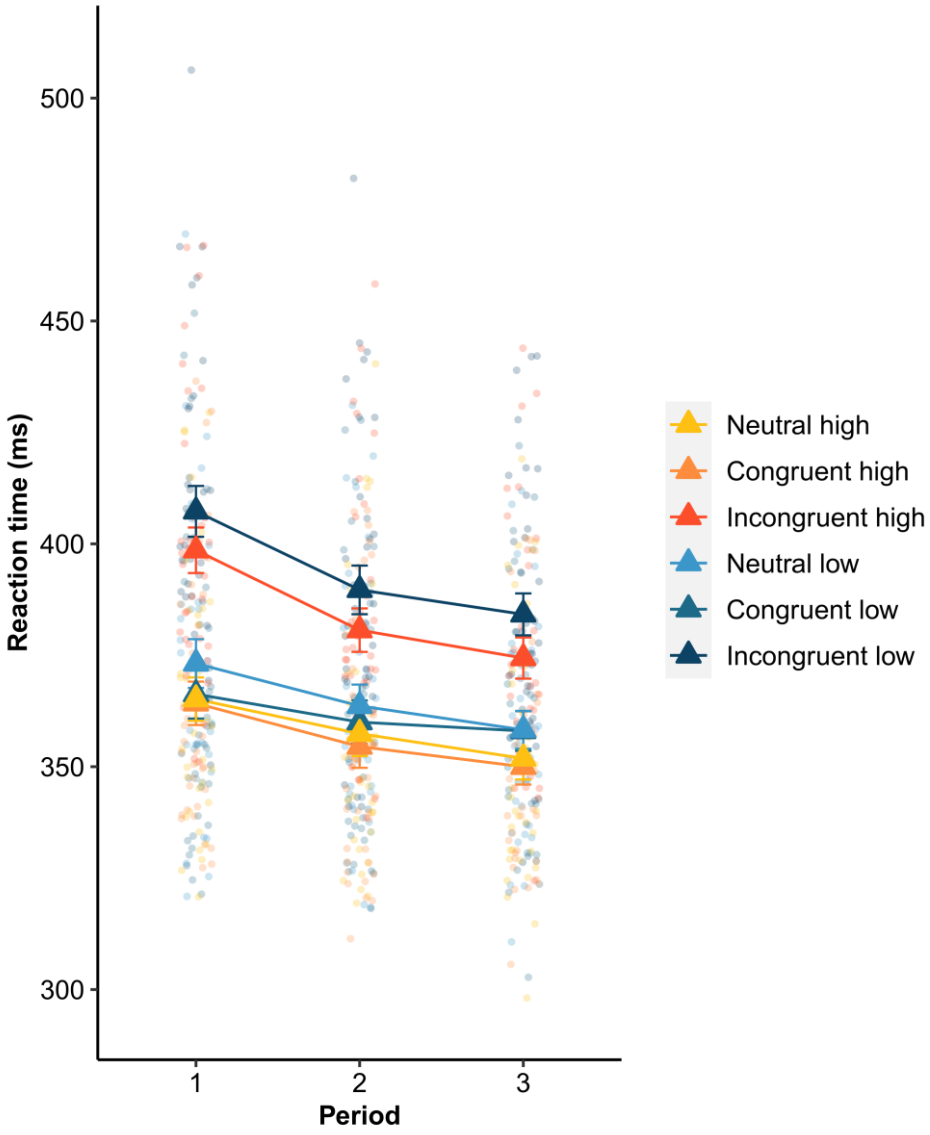

Figure 2. Main task performance measured by RTs over the course of the task. Blue colors represent performance on the low-probability trials and orange colors represent performance on the high-probability trials. Congruency is indicated by color gradient, from lightest to darkest respectively for neutral, congruent, and incongruent trials. Faded circle shapes show individual data points. Participants performed better on high-probability and congruent trials, while their performance was poorer on the low-probability and incongruent trials. RTs between high- and

low-probability trials differed in all congruency conditions indicating successful procedural learning. In both probability conditions, performance on incongruent trials was poorer compared with performance on the congruent ones, indicating the congruency effect. Error bars represent Standard Error of the Mean (SEM).

Accuracy – We observed a similar overall pattern in accuracy as in RTs (Figure 3). Both the procedural learning effect and the flanker congruency effect were present (main effect of Probability, $F(1, 35) = 55.857$, $p < .001$, $\eta_p^2 = .615$; main effect of Congruency, $F(2, 70) = 65.41$, $\varepsilon = .762$, $p < .001$, $\eta_p^2 = .651$, respectively; Figure 3), both appearing constant over time (non-significant Probability * Time and Congruency * Time interactions, $F(2, 70) = 2.06$, $p = .135$, $\eta_p^2 = .056$, $F(4, 140) = 2.28$, $p = .064$, $\eta_p^2 = .061$, respectively). Interestingly, however, a significant—but less strong—Probability * Congruency effect was observed ($F(2, 70) = 3.55$, $p = .034$, $\eta_p^2 = .092$). Based on the pair-wise comparisons, this effect was possibly driven by the poor performance on incongruent low-probability trials (88.8%; accuracy in all other conditions was ≥ 91.5%), leading to a larger flanker congruency effect on low-probability trials compared with the high-probability ones ($p < .001$). The magnitude of learning did not differ across flanker types (all ps ≥ .269). The main effect of Time and the triple interaction did not reach significance ($F(2, 70) = 0.15$, $p = .308$, $\eta_p^2 = .073$, $F(4, 140) = 37.77$, $\varepsilon = .755$, $p < .001$, $\eta_p^2 = .519$, respectively). Thus, we found a weak effect suggesting the interaction of procedural learning and interference suppression. Nevertheless, the effect seemed to be driven by the poor performance on the incongruent low-probability trials possibly due to the increased cognitive load.

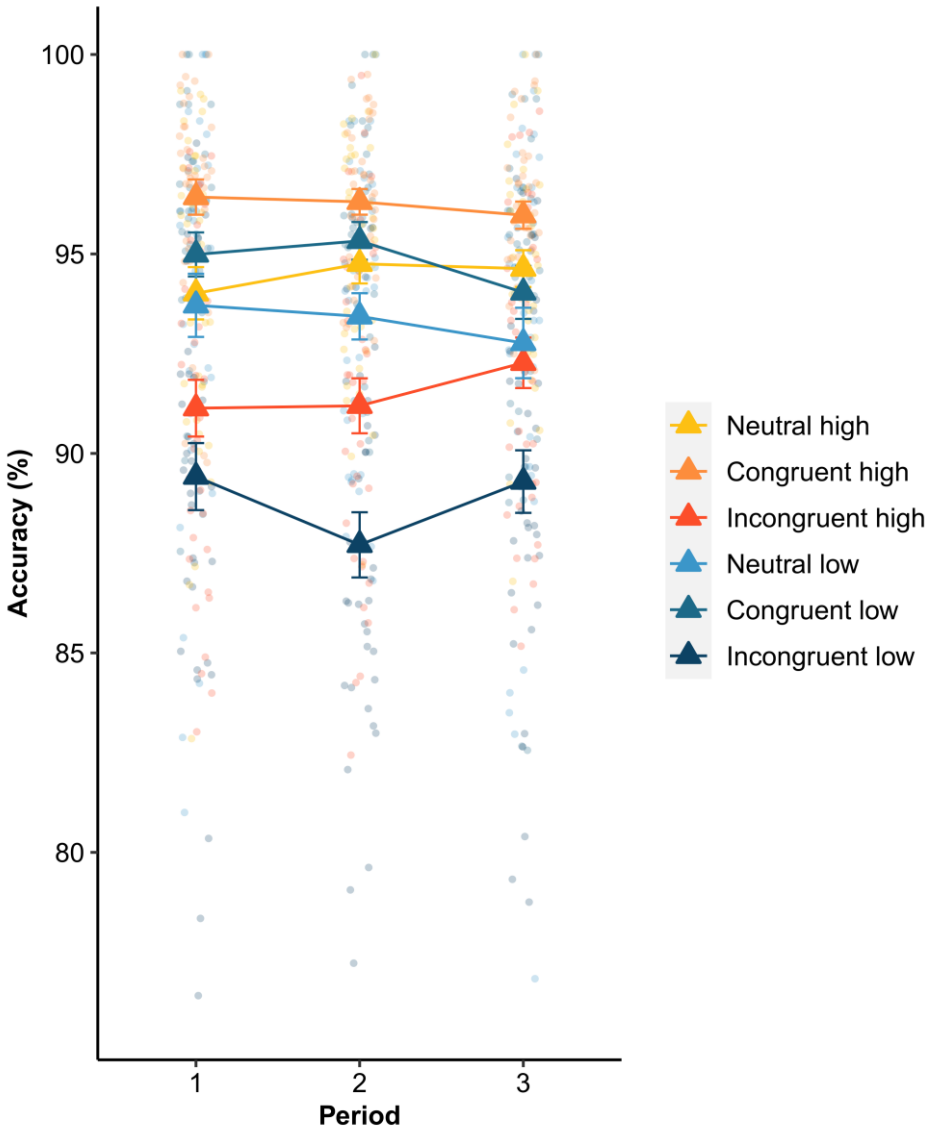

Figure 3. Main task performance measured by accuracy over the course of the task. Blue colors represent performance on the low-probability trials and orange colors represent performance on the high-probability trials. Congruency is indicated by color gradient, from lightest to darkest respectively for neutral, congruent, and incongruent trials. Faded circle shapes show individual data points. Participants committed more errors on low-probability and incongruent trials. Performance on high- and low-probability trials differed in all congruency conditions, indicating successful procedural learning. In both probability conditions, the flanker congruency effect was observed between the congruent and incongruent conditions. Error bars represent Standard Error of the Mean (SEM).

Interim summary – Overall, our RT findings suggest that procedural learning and interference suppression operate in parallel when simultaneously involved in the task. In other words, interaction between these processes seemed to be absent in the present task suggesting an independent relationship, in line with some parts of previous literature (Jiménez, Abrahamse, et al., 2020; Jiménez, Méndez, et al., 2020). From another point of view, these findings also highlight the robust nature of procedural learning (e.g., Horváth et al., 2020; Nemeth et al., 2011; Tóth-Fáber et al., 2020) as it appeared to be resistant to the increased amount of conflict in the task. Importantly, however, the analysis of accuracy revealed that procedural learning and interference suppression may interact with each other. The congruency effect was larger on the improbable trials, suggesting that when both uncertainty and conflict are higher due to the trial being improbable and incongruent, respectively, they affect response selection in an additive way. Alternatively, the two underlying processes may interfere or even compete for response selection resulting in an impaired performance (see also Bocanegra & Hommel, 2014).

Is there an interaction between interference suppression and procedural learning when the conflict-driven adjustment effect is considered?

Reaction time – Conflict-driven adjustment was measured by the CSE. In the case of a canonical CSE, the congruency effect is reduced following an incongruent trial than a congruent one. The influential effect of previous trial congruency was shown by the significant Probability * Current * Previous interaction ($F(1, 33) = 16.67$, $p < .001$, $\eta_p^2 = .336$; Figure 4). Pairwise comparisons revealed the following effects. In the case of low-probability trials, the congruency effect following an incongruent trial appeared reduced compared with following a congruent one ($p = .004$; 21 ms vs. 38 ms). Interestingly, in the case of high-probability trials this effect seemed to be reversed and the congruency effect was slightly larger following an incongruent trial compared with following a congruent one ($p = .023$; 33 ms vs. 27 ms). The ANOVA also revealed a significant main effect of current trial congruency in the expected direction; all other main effects and interactions were non-significant (all ps $\geq .059$, [the p value of the trend-level main effect of Probability]).

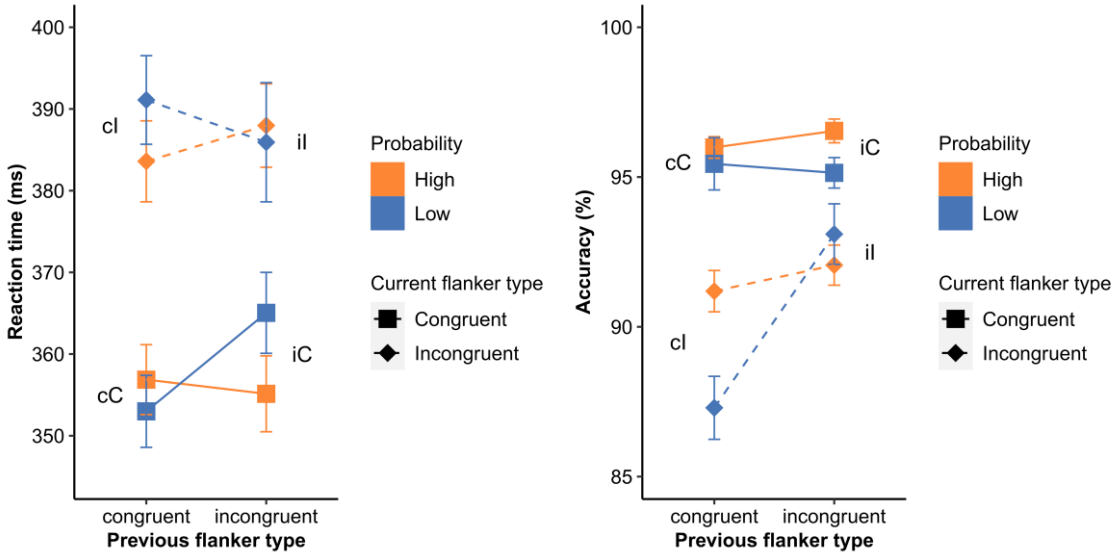

Figure 4. Congruency Sequence Effect in the task. CSE was examined for the whole session. Blue represents performance on low-probability trials and orange represents performance on high-probability trials. Current trial congruency is indicated by different shapes and lines and capital letters: congruent trials are represented by squares, solid lines, and letter 'C', and incongruent trials are represented by rhombuses, dashed lines, and letter 'I'. Previous flanker type is indicated on the horizontal axis and by lowercase letters ('c' = congruent, 'i' = incongruent). The vertical axis shows performance (left side: RTs, right side: accuracy). In RTs, CSE was apparent on low-probability trials; nevertheless, an effect opposing the canonical direction of the CSE also emerged on the high-probability trials. In accuracy, CSE was found only on the low-probability trials. Error bars represent Standard Error of the Mean (SEM).

Accuracy – This analysis also revealed a significant Probability * Current * Previous interaction ($F(1, 33) = 10.81$, $p = .002$, $\eta_p^2 = .247$; Figure 4). Pairwise comparisons showed that the congruency effect measured on low-probability trials was reduced following an incongruent trial ($p = .002$; 2.1% vs. 8.2%), whereas such effect was not present on the high-probability trials ($p = .635$; 4.8% vs. 4.5%). The ANOVA also revealed significant main effects of Probability and Current trial congruency in the expected direction ($F(1, 33) = 9.01$, $p = .005$, $\eta_p^2 = .215$; $F(1, 33) = 55.44$, $p < .001$, $\eta_p^2 = .624$, respectively). The significant main effect of Previous trial congruency ($F(1, 33) = 26.56$, $p < .001$, $\eta_p^2 = .446$) showed that incongruent trials lead to higher accuracy irrespective of current trial type, possibly reflecting the strong CSE effect measured on low-probability trials. The Probability * Previous and the Current * Previous

interactions reached significance ($F(1, 33) = 5.60$, $p = .024$, $\eta_p^2 = .145$; $F(1, 33) = 9.62$, $p = .004$, $\eta_p^2 = .226$, respectively); nevertheless, as these effects possibly contain the covert influence of current trial properties, we do not discuss them here. The Probability * Current interaction appeared as non-significant ($F(1, 33) = 0.28$, $p = .601$, $\eta_p^2 = .008$). Altogether, while the CSE was present only on the low-probability trials, accuracy in general seemed to be more sensitive to previous trial congruency compared with RTs.

Interim summary – Opposing the analysis of the learning effect and the congruency effect without taking into account conflict-driven adjustment effects, the analysis of the CSE revealed an interactive relationship between these processes. Interestingly, while the CSE appeared in the case of low-probability trials as expected, it was reversed for high-probability trials in RTs and absent in accuracy. These findings suggest that a hampering effect between procedural learning and interference suppression may be present. In more detail, it is presumable that when a trial cannot be predicted, conflict adaptation processes can exert their effect on response selection, thus the CSE appears on improbable trials. On the other hand, when a trial can be predicted, both procedural learning and conflict adaptation processes are involved in response selection, however, their additional effect results in an overshoot or overcontrol leading to worse performance in fact. A similar effect was found by Bocanegra and Hommel (2014) who proposed that in a predictable environment, the additional involvement of cognitive control processes hinders performance. Notably, this effect was present only for RTs and was absent in accuracy. The present study did not aim to and cannot clarify the differences emerged across RTs and accuracy; thus, further studies are needed to target this question.

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APPENDIX II: SUPPLEMENTARY MATERIAL FOR STUDY 2

Supplementary material of the manuscript entitled

Perceiving structure in unstructured stimuli: Implicitly acquired prior knowledge impacts the processing of unpredictable transitional probabilities

Authors: Andrea Kóbor, Kata Horváth, Zsófia Kardos, Dezso Nemeth, Karolina Janacsek

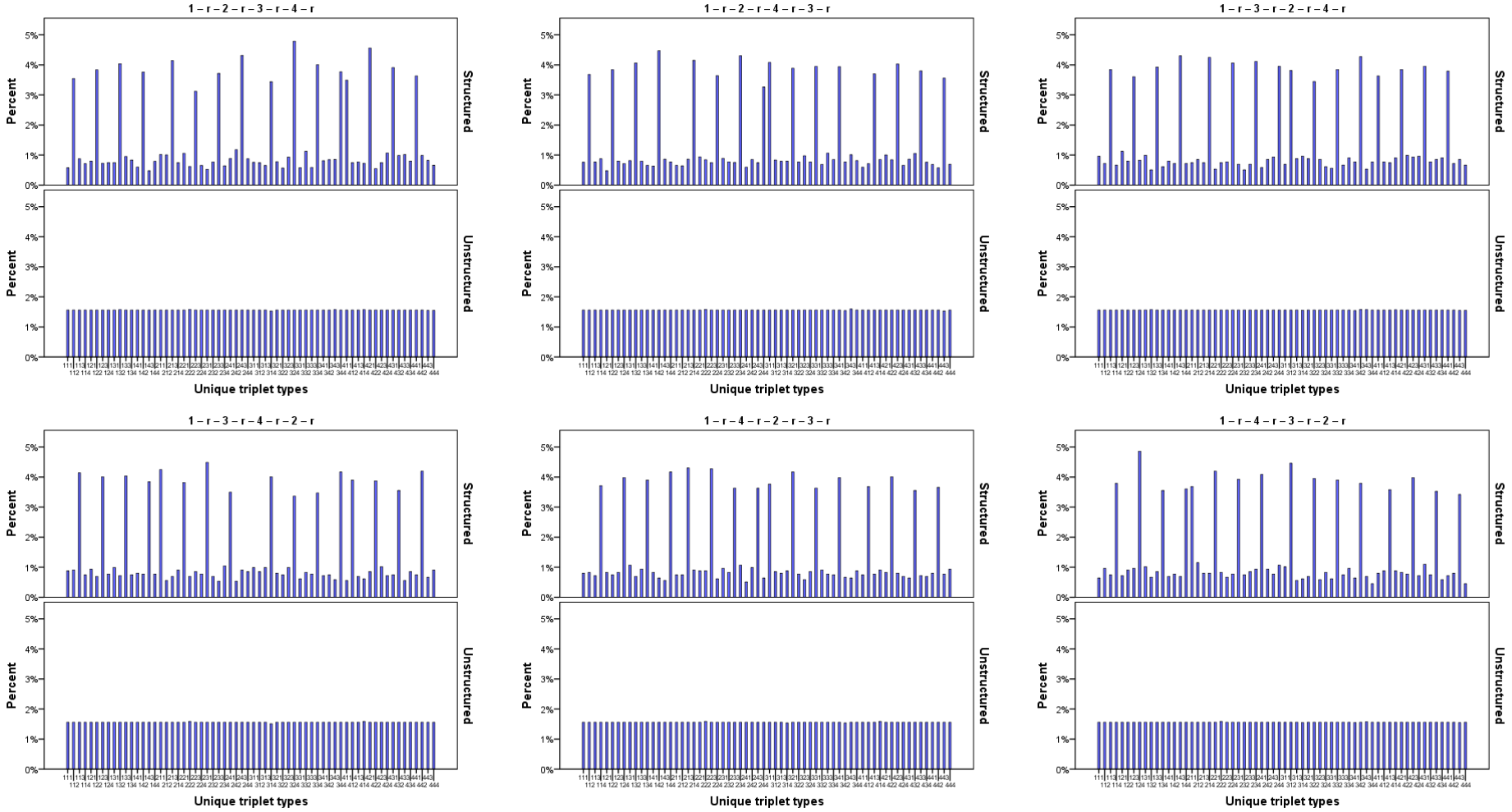

Figure S1. Distribution of triplet frequencies for the 64 unique triplet types in the entire sample (N = 50) according to the six unique ASRT sequences, separately for the structured and unstructured sequences. In the structured sequences, among the 64 unique triplets, 16 are high-probability triplets and 48 are low-probability ones; the formers are indicated by the higher bins. There is partial overlap across the six unique ASRT sequences in terms of the actual high-probability triplets. The distribution of triplet frequencies is flat in the unstructured sequences, as each triplet occurs with equal probability.

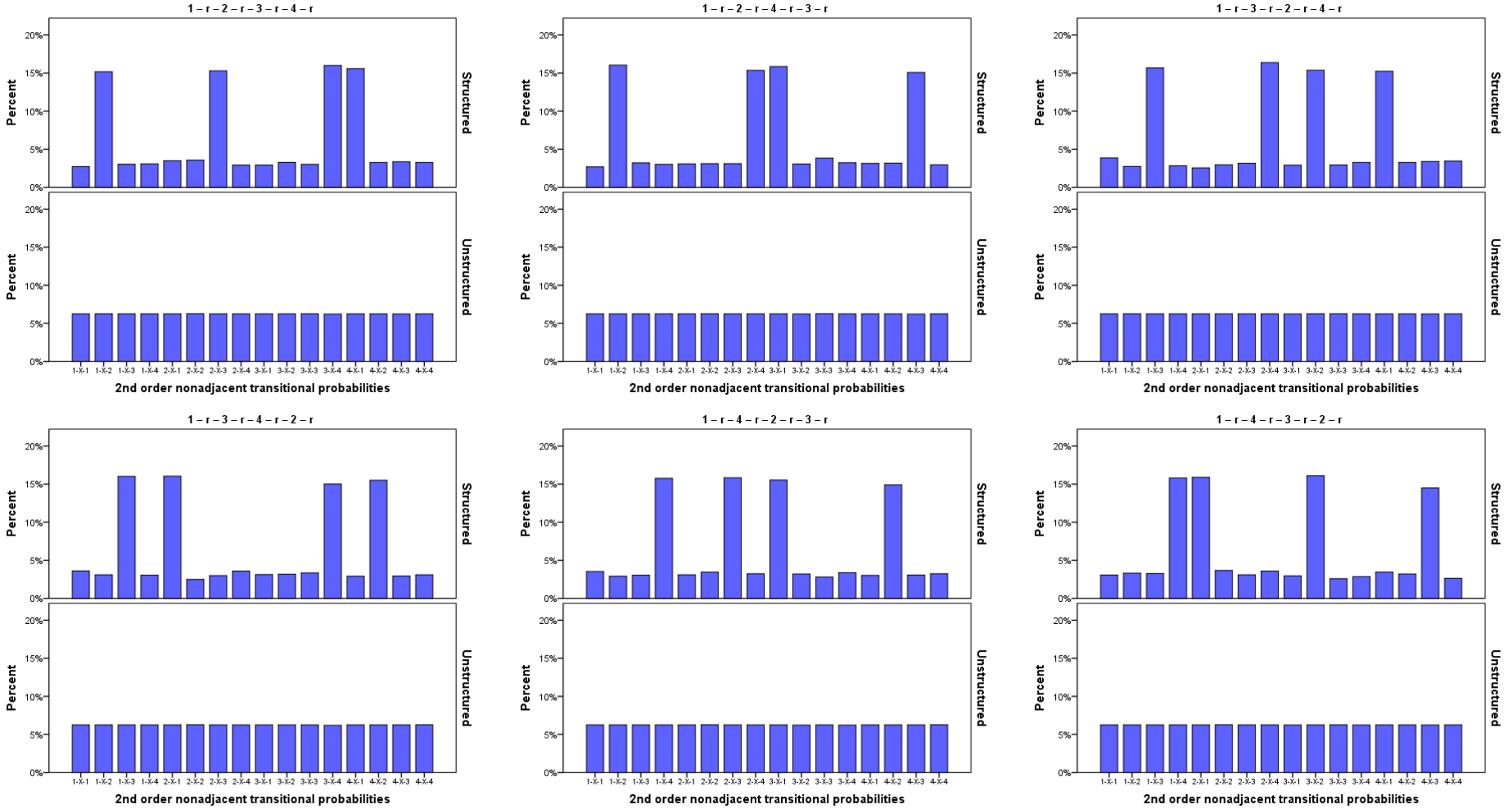

Figure S2. Distribution of 2nd order nonadjacent transitional probabilities (16 triplet categories, e.g., 1 – X – 3, 3 – X – 2; X denotes the middle trial of the triplet) in the entire sample (N = 50) according to the six unique ASRT sequences, separately for the structured and unstructured sequences. In the structured sequences, four triplet categories include all the high-probability triplets in the given unique ASRT sequence, indicated by the higher bins. There is partial overlap across the six unique ASRT sequences in terms of the high-probability triplet categories. The distribution of 2nd order nonadjacent transitional probabilities is flat in the unstructured sequences, as each of them occurs with equal probability.

APPENDIX III: SUPPLEMENTARY MATERIAL FOR STUDY 3

Supplementary Materials for 'Divided Attention does not affect the acquisition and consolidation of transitional probabilities'

Kata Horváth, Csenge Török, Orsolya Pesthy, Dezso Nemeth, Karolina Janacsek

1. Raw (non-standardized) RT performance on random high-probability vs. random-low probability trials

Here we report performance on the random high-probability vs. random low-probability trials (i.e. statistical learning contrast) measured by raw RTs (Figure S1). A mixed-design ANOVA containing EPOCH (1-5 for the Learning Phase, 5-6 for the 12-hr delay) and TRIAL TYPE (random high-probability vs. random low-probability) as within-subject factors and INSTRUCTION (cued vs. uncued) and SLEEP (sleep vs. no-sleep) as between-subject factors was conducted for the Learning Phase as well as for the 12-hr post-learning offline delay. Below we highlight and summarize only those results that are relevant for the primary analyses and interpreted in the main text. For the detailed results see Table S1.

The Cued group showed significantly slower RTs on average compared with the Uncued group both in the Learning phase and after the 12-hour delay (significant main effect of INSTRUCTION; $p < .001$, $p = .011$, respectively). Slower RTs in the Cued group could suggest a higher attentional load, which could also indicate that the divided attention manipulation was effective, in line with the performance on sequence trials (see section 2, Table S2, and Figure S2 below) and on the post-block sequence report task (for more details see Results in the main text). The average RTs did not differ across the four subgroups when the SLEEP factor was also taken into account (the INSTRUCTION x SLEEP interaction not significant), however, the trajectory of average RTs differed across the four subgroups (significant EPOCH x INSTRUCTION x SLEEP interaction). Importantly, this latter effect did not involve the TRIAL TYPE factor, suggesting that the effect was independent of statistical learning, and therefore will not be discussed further. To control for group differences in average RTs in the subsequent analyses, raw RTs were standardized as presented in the main text (for more details see Statistical Analysis and Results). Nevertheless, it is important to note, that the TRIAL TYPE-related effects (that is, those related to statistical learning) in the raw RT ANOVAs are

consistent with the results on standardized RTs presented in the main text as well as with the Bayesian analyses presented below in Table S4.

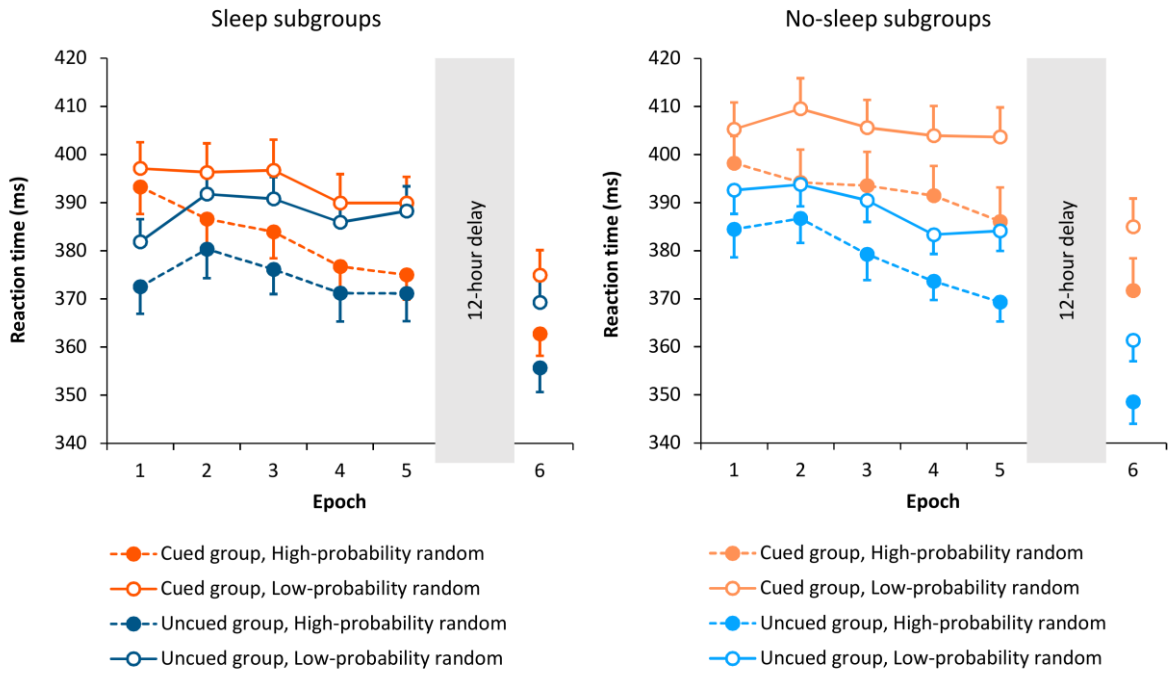

Figure S1. Raw reaction times (RTs) for the random high-probability and random low-probability trials over the time course of learning, separately for the four subgroups. The Cued group showed slower RTs on average compared with the Uncued group, while the difference between the random high- and low-probability trials, that is statistical learning, did not differ across groups. Error bars represent the standard error of the mean (SEM).

Table S1. ANOVA results for raw RTs on random high-probability vs. random low-probability trials.

	EPOCH			TRIAL TYPE			EPOCH * TRIAL TYPE			INSTRUCTION		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	10.737	< **.001**	.105	221.812	< **.001**	.707	5.072	**.001**	.052	5.518	**.021**	.021
12-hr delay	115.178	< **.001**	.556	196.530	< **.001**	.681	2.840	.095	.030	6.699	**.011**	.068

	EPOCH x INSTRUCTION			TRIAL TYPE x INSTRUCTION			EPOCH x TRIAL TYPE x INSTRUCTION			SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	1.206	.307	.013	0.002	.963	< .001	0.652	.625	.007	1.880	.174	.020
12-hr delay	1.890	.173	.020	0.002	.961	< .001	0.037	.848	< .001	0.341	.561	.004

	EPOCH x SLEEP			TRIAL TYPE x SLEEP			EPOCH x TRIAL TYPE x SLEEP			INSTRUCTION x SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	0.504	.654	.005	0.154	.696	.002	0.358	.839	.004	0.645	.424	.007
12-hr delay	1.326	.253	.014	0.006	.940	< .001	0.001	.991	< .001	2.740	.101	.029

	EPOCH x INSTRUCTION x SLEEP			TRIAL TYPE x INSTRUCTION x SLEEP			EPOCH x TRIAL TYPE x INSTRUCTION x SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	2.842	**.046**	.030	2.743	.101	.029	.221	.927	.002
12-hr delay	0.062	.803	.001	0.645	.424	.007	0.176	.676	.002

Note. *P* values < .05 are **bold-faced**. The main effect of EPOCH can indicate RT changes during the task, irrespective of trial type. The main effect of TRIAL TYPE can indicate RT differences between the random high-probability and random low-probability trial types (that is, statistical learning), while the EPOCH x TRIAL TYPE interaction can indicate different trajectories for these trial types in the time course of learning. The main effect of INSTRUCTION can indicate differences in average RTs between the Uncued and Cued groups, irrespective of trial type, while the EPOCH x INSTRUCTION interaction can indicate group differences in the time course of average RTs. The TRIAL TYPE x INSTRUCTION interaction can indicate trial type-related differences between the Uncued and Cued groups, and the EPOCH x TRIAL TYPE x INSTRUCTION interaction can indicate such differences in the time course of learning. The main effect of SLEEP can indicate differences in average RTs between the Sleep and No-sleep subgroups, irrespective of the cuing manipulation and trial type, while the EPOCH x SLEEP interaction can indicate group differences in the time course of average RTs. The TRIAL TYPE x SLEEP interaction can indicate trial type-related differences between the Sleep and No-sleep subgroups, irrespective of the cuing manipulation, and the EPOCH x TRIAL TYPE x SLEEP interaction can indicate such differences in the time course of learning. The INSTRUCTION x SLEEP interaction can indicate differences in average RTs across the four subgroups, irrespective of trial type, while the EPOCH x INSTRUCTION x SLEEP interaction can indicate differences in the time course of average RTs across the four subgroups. Finally, the TRIAL TYPE x INSTRUCTION x SLEEP interaction can indicate trial type-related differences across the four subgroups, while the EPOCH x TRIAL TYPE x INSTRUCTION x SLEEP interaction can indicate such differences in the time course of learning.

2. Standardized RTs for sequence trials compared with random trials across the four subgroups

To ensure that participants in the Cued group indeed followed the instruction regarding the sequence trials and, therefore, the divided attention manipulation was successful, we tested the performance on the sequence vs. random trials, irrespective of trial probability (that is, random trials included both high- and low-probability trials), across the four subgroups (see Figure S2).

Here we report mixed design ANOVAs on standardized RTs with EPOCH (1-5 for the Learning Phase; 5 vs. 6 for the 12-hr delay) and TRIAL TYPE (Sequence vs. Random) as within-subject factors and INSTRUCTION (Uncued vs. Cued) and SLEEP (Sleep vs. No-sleep) as between-subject factors (for detailed results see Table S2). Importantly, these ANOVAs revealed a significant TRIAL TYPE x INSTRUCTION interaction both in the Learning and the Testing phases (p = .001, p = .002, respectively). The Cued group showed faster responses on the sequence trials compared with the random ones during the entire experiment (all ps < .001). In contrast, the Uncued group showed similar RTs on the sequence vs. random trials (Learning Phase: p = .913, 12-hr delay: p = .094). Overall, this result suggests that the Cued group followed the divided attention instruction throughout the task, and thus the manipulation was effective.

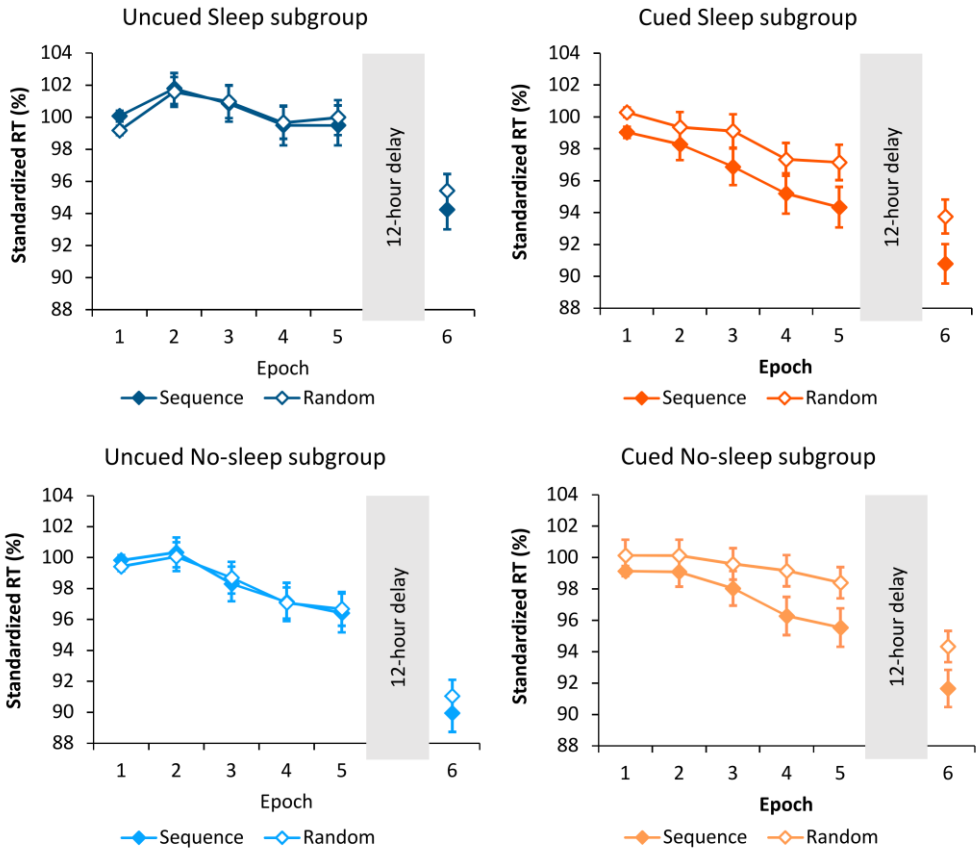

Figure S2. Standardized RTs for the sequence and the random trials (irrespective of trial probability) over the time course of learning across the four subgroups. While the Uncued Sleep and No-sleep subgroups showed similar RTs for trials in the sequence position as for trials in the random position, the Cued Sleep and No-sleep subgroups responded faster to the sequence trials compared with the random trials, indicating the effect of divided attention instruction. Error bars represent the SEM.

Table S2. ANOVA results for standardized RTs on sequence vs. random trials.

	EPOCH			TRIAL TYPE			EPOCH * TRIAL TYPE			INSTRUCTION		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	18.531	**< .001**	.169	11.700	**.001**	.113	5.789	**< .001**	.059	2.576	.112	.027
12-hr delay	131.840	**< .001**	.589	31.680	**< .001**	.256	1.598	.209	.017	.788	.377	.008

	EPOCH x INSTRUCTION			TRIAL TYPE x INSTRUCTION			EPOCH x TRIAL TYPE x INSTRUCTION			SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	1.643	.191	.018	12.787	**.001**	.122	1.121	.344	.012	0.482	.489	.005
12-hr delay	4.808	**.031**	.050	10.486	**.002**	.102	1.748	.189	.019	1.845	.178	.020

	EPOCH x SLEEP			TRIAL TYPE x SLEEP			EPOCH x TRIAL TYPE x SLEEP			INSTRUCTION x SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	0.438	.677	.005	0.001	.993	< .001	0.143	.951	.002	3.302	.072	.035
12-hr delay	1.041	.310	.011	0.049	.826	.001	0.024	.877	< .001	5.358	.023	.055

	EPOCH x INSTRUCTION x SLEEP			TRIAL TYPE x INSTRUCTION x SLEEP			EPOCH x TRIAL TYPE x INSTRUCTION x SLEEP		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
Learning Phase	2.353	.089	.025	0.006	.939	.006	0.664	.596	.007
12-hr delay	0.154	.695	.002	0.001	.979	< .001	0.167	.683	.002

Note. *P* values < .05 are **bold-faced**. For how to interpret these effects, please see the note of Table S1, with the only difference that the ANOVAs reported here contrasted sequence vs. random trials, instead of random high- vs. random-low probability trials. The ANOVAs revealed some differences in average RTs and their trajectories across groups (INSTRUCTION x SLEEP, EPOCH x INSTRUCTION x SLEEP, and EPOCH x INSTRUCTION interactions). Importantly, none of these effects involved the TRIAL TYPE factor and, therefore, it will not be further discussed. The interested reader could gain further insights into these effects on average RTs by inspecting Figure S2.

3. Acquisition and consolidation of statistical knowledge measured by accuracy

Similar ANOVAs were conducted for the statistical learning scores calculated on accuracy data as the ones reported in the main text using standardized RT data (see Results). The details of

these ANOVAs can be found in Table S3. While most of the effects are consistent with the results on the standardized as well as raw RT data, the main effect of SLEEP and the EPOCH x SLEEP interaction during the 12-hr delay revealed an additional trend (p = .079; p = .061, respectively). Learning scores in the Testing Phase appeared to be slightly decreased when the offline delay contained wake activity (p = .023; end of the Learning Phase: 3.6%; Testing Phase: 1.6%) compared with sleep (p = .693; end of the Learning Phase: 3.7%; Testing Phase: 4.1%). This additional trend suggests a beneficial effect of sleep on consolidation regardless of attention manipulation, contrary to the standardized and raw RT effects (see the Results section in the main text and Table S4 below, respectively). This difference might be originating from accuracy and RT measures capturing different aspects of learning/memory: It has been previously argued that while RTs could reflect involuntary processes, accuracy could reflect voluntary and more controlled processes [1]. It is important to note, however, that this accuracy effect should be treated with caution as it was not supported by the Bayesian analysis (see Table S4). Moreover, previous studies reporting accuracy data found retention of the acquired knowledge [2–5], irrespective of post-learning delay activity [2,4]. Therefore, further studies are needed to confirm or disprove this effect.

Table S3. ANOVA results for statistical learning scores calculated on the accuracy data.

	INTERCEPT			EPOCH			INSTRUCTION			EPOCH x INSTRUCTION		
	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2
Learning Phase	88.848	**< .001**	.491	5.506	**< .001**	.056	.802	.373	.009	1.336	.256	.014
12-hr delay	80.127	**< .001**	.466	1.772	.186	.019	1.142	.288	.012	0.119	.731	.001
	SLEEP			EPOCH x SLEEP			INSTRUCTION x SLEEP			EPOCH x INSTRUCTION x SLEEP		
	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2
Learning Phase	0.415	.521	.005	1.497	.202	.016	0.011	.918	< .001	1.248	.290	.013
12-hr delay	3.150	.079	.033	3.602	.061	.038	0.003	.956	< .001	0.295	.588	.003

Note. *P* values < .05 are **bold-faced**. Since the ANOVAs are conducted on learning scores, the INTERCEPT can indicate significant learning. The main effect of INSTRUCTION can indicate INSTRUCTION differences in the learning scores. The main effect of EPOCH can indicate changes in the learning scores during the task, while the INSTRUCTION x EPOCH interaction can indicate INSTRUCTION differences in the time course of learning. The main effect of SLEEP can indicate Sleep and No-sleep SLEEP differences irrespective to the level of intention

to learn. The INSTRUCTION x SLEEP interaction can indicate the SLEEP differences within the main INSTRUCTIONs, while the INSTRUCTION x EPOCH x SLEEP interaction can indicate these differences in the time course of learning. For more details, see the main text of the manuscript.

4. Bayesian ANOVAs conducted on the raw RT and accuracy data

Finally, here we present all BF_{01} and $BF_{Exclusion}$ values for the Bayesian ANOVAs conducted on the raw RT and accuracy data (see Table S4). Please note that although raw RTs are presented separately for the random high-probability and random low-probability trials above (Figure S1, Table S1), here we report the Bayesian ANOVA conducted on learning scores for better comparability with the analysis presented in the main text as well as with the analysis conducted on accuracy data.

These analyses are in line with and support most results of the frequentist analyses (i.e., null-hypothesis significance testing). Notably, the slight trend for the effect of sleep on consolidation found in the accuracy data (see the previous section above) is not confirmed by the Bayesian ANOVA, supporting the conclusion that this effect should be treated with caution.

Table S4. Bayesian ANOVA results for statistical learning scores calculated on the raw RT and accuracy data.

Model	Raw RTs				Accuracy			
	Learning Phase		12-hr delay		Learning Phase		12-hr delay	
	BF_{01}	$BF_{Exclusion}$	BF_{01}	$BF_{Exclusion}$	BF_{01}	$BF_{Exclusion}$	BF_{01}	$BF_{Exclusion}$
NULL MODEL	1.000	-	**1.000**	-	1.000	-	**1.000**	-
EPOCH	**0.029**	**0.081**	1.478	3.278	**0.002**	**4.629e^{-4}**	2.515	4.255
INSTRUCTION	7.676	19.246	5.320	13.109	3.412	6.802	3.437	7.752
EPOCH x INSTRUCTION	6.567	113.944	34.553	30.268	0.018	5.747	35.247	20.408
SLEEP	7.278	17.832	5.289	12.947	5.504	12.500	1.460	2.740
EPOCH x SLEEP	10.139	175.568	35.192	32.186	0.074	20.408	2.945	2.994
INSTRUCTION x SLEEP	102.293	52.811	82.730	48.507	89.200	41.667	18.341	14.085
EPOCH x INSTRUCTION x SLEEP	94290.995	2262483.216	9499.680	1037.228	13.192	1000.000	512.674	11.111

Note. The BF_{01} value of the best fitting model is **bold-faced**. In Bayesian ANOVAs, BF_{01} values reflect how well a model fits the data: The smaller the BF_{01} value is, the better the model predicts the data. BF_{01} value of the null model, which contains the grand mean only is always 1 [6]. The $BF_{Exclusion}$ value quantifies the evidence for the inclusion of a factor or an interaction of factors in the model and can be interpreted in the same direction as BF_{01} values (i.e. the smaller the value, the stronger the evidence for including the given factor). For how to interpret the main effects and interactions see the note of Table S3.

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APPENDIX IV: SUPPLEMENTARY MATERIAL FOR STUDY 4

Supplementary information for the manuscript entitled

'Inhibitory control hinders habit change'

Authors: Kata Horváth, Dezso Nemeth, Karolina Janacsek

Table of contents

Supplementary introduction: Behavioral and neural characteristics of habit learning across human and animal studies

The definition of habits was originally described in animal studies[1,2], highlighting them as behaviors that are elicited by environmental stimuli to which they have become strongly tied and that become insensitive to both outcome (reward) devaluation and contingency degradation[3]. Importantly, it has been recognized that these features and the experimental methods developed to assess habits in animals may not be directly translatable to and likely not sufficient to capture habits in humans[2,4]. Humans are capable of performing tasks without rewards—simply because they are instructed to do so. Therefore, the habitual nature of the acquired associations can be tested using a broader range of methods compared to animals where the outcome devaluation and contingency degradation tests are needed to establish the presence of habitual behaviors[2,5,6]. Moreover, in some cases humans might even use alternative or additional cognitive mechanisms to solve the same task compared to animals (e.g., healthy humans solve a simple concurrent discrimination task using declarative learning processes, while monkeys use habit learning processes[7–9]), further highlighting that different approaches should be favored when testing human habit learning. Indeed, probabilistic classification, sequential decision making, and (motor) sequence learning tasks have all been used to test aspects of habitual behavior in humans as they show similarities with more classical habit learning tasks both on behavioral and neural level[10–15]. (For recent successful attempts at identifying habitual behaviors in more classical habit learning tasks, the outcome devaluation test and the reversal learning task, see[16,17] and the Discussion in the main text.)

Here we present the major similarities—both behavioral and neural—between sequence learning tasks and other commonly used habit learning tasks and argue that despite rarely being employed in the animal literature, sequence learning tasks, including the ASRT used in our study, are valid tools to measure habit learning and change in humans.

On the **behavioral level**, habits in humans are often defined by a collection of attributes that include (i) gradual learning over extended practice; (ii) learning can occur implicitly (i.e., without awareness of what was learned and without conscious control over the acquired knowledge); and (iii) the learned behavior is performed automatically (e.g., without full attention, such as under distraction), even when the behavior becomes no longer relevant (e.g., when environmental contingencies or the outcomes/rewards of the behavior change)[2,18–20]. Notably, it has been recognized that these characteristics of habits do not always cluster together; it is possible that some of these characteristics emerge without others. For example, if

no rewards/reinforcers are given, the other characteristics of habit learning and behavior can still be captured[2,20]. In the next paragraphs, we will discuss how learning and the acquired knowledge in sequence learning tasks and the ASRT, in particular, show many of the defining attributes of habits.

First, habits are learned **gradually, over an extended training period**[4,18]. Learning in SRT-like tasks is likewise gradual and based on extended practice[21]. In the present study, both the Learning phase and the Rewiring phase contained 45 blocks, with 80 stimuli and button presses in each block (excluding the first 5 random trials), that is, the associations were practiced over 3600 trials in each phase. This added up to around an hour and a half of practice per session with breaks between blocks (for more details see the Methods and Supplementary methods sections in the revised MS and SI, respectively). This amount of practice constitutes an extensive training compared to a range of other ASRT studies that focused mainly on earlier phases of learning (with ~1600-2000 trials per session) [e.g., 22–24]. It has been previously shown in healthy human adults that an extended practice of 3600 trials leads to persistent memories of the acquired associations even after a one-year delay that did not include any further practice[25]. Thus, while fewer trials can be sufficient for the initial acquisition of the associations embedded in the task, a more extended practice can help strengthen and automatize the acquired knowledge (see also below). This is why we chose 3600 trials per session in the present study.

Second, habits can be **acquired and performed implicitly,** that is, without awareness of or conscious control over the acquired knowledge[2,4,26]. While learning in deterministic sequence learning tasks often reaches awareness (i.e., participants consciously recognize the repeating sequence) [e.g., 27–29], numerous studies have shown that learning in the ASRT task typically remains fully implicit. The implicit nature of learning and the acquired knowledge can be probed by verbalization, generation, and recognition tests[30]. The verbalization test probes whether participants can verbally declare any task regularities that they may have noticed/learned [e.g., 31,32]. The generation test probes whether participants can consciously control the acquired knowledge by asking them first to generate the regularity present in the task and then generate a new series of responses that do not contain the learned regularities [23,33,34]. In the recognition test, participants are presented with the acquired associations and are asked to decide whether they recognize them or not[15,35]. Based on an extensive list of studies that used verbalization, generation, and/or recognition tests, a recent review conclusively showed that learning and the acquired knowledge remains implicit in the ASRT task [30].

In our study, we used both a generation and a recognition task to test whether participants gained awareness about and conscious control over the acquired knowledge. In the Free generation task, we asked participants to think about the first day then the second day of practice (in a counterbalanced order) and then try to generate the order in which the stimuli appeared. The results showed that they produced the acquired associations at a similar rate for both experimental phases; thus, they did not have conscious control over the acquired knowledge. In the Triplet sorting task, participants were presented with all unique associations (triplets) learned during the Learning phase and the Rewiring phase, separately, and were asked to decide whether the presented associations occurred frequently or not during the given experimental phase. Performance was similarly at chance level for all trial types for both phases (i.e., triplets that were high-probability in the Learning phase but became low-probability in the Rewiring phase, or vice versa, separately in Go and No-go trials), showing that the acquired knowledge was implicit. Further details on these tasks and analyses can be found in the Supplementary results section. We believe that these two measures together with previous studies using the same task and similar samples prove that the acquired associative knowledge in the ASRT task is implicit.

Third, habits are **performed automatically**. For sequence learning tasks, including the ASRT task, a growing body of evidence shows that divided attention[23,36], cognitive load[37], or a secondary task[38] does not affect the learning and expression of associative knowledge. Additionally, using preparatory event-related brain potentials, a recent ASRT study[31] showed that anticipation and processing of stimuli that were predictable based on the acquired associations required less attentional resources compared to unpredictable stimuli; thus, anticipation and processing of the upcoming stimuli were automatic and sensitive to the acquired associative knowledge.

As noted above, in sequence learning tasks, alike most human cognitive tasks, participants provide responses simply because they are instructed to do so. Therefore, the mere fact of responding to a stimulus does not necessarily provide useful information about the automatic stimulus-response (S—R) links that participants learn in these tasks. Instead, automaticity can be assessed using the characteristics of responses such as response speed. For example, in the ASRT task, participants acquire and their responses become driven by probability-based associations between runs of three consecutive stimuli: in some cases, the current stimulus (third of the three) can be predicted with a higher probability based on the two previous stimuli, while in other cases, this predictive probability is low. Once acquired, the first

stimulus automatically elicits the high-probability association when the third stimulus is presented, resulting in faster reaction times than for those third stimuli that are less predictable by the first ones. Thus, S—R links are developed in this task where the speed of the current response is influenced by the combination of the previous and the current stimuli (instead of the current stimulus alone). Indeed, in the present study, participants answered increasingly faster to high-probability stimuli than to low-probability ones, indicating the development of automatic associations as learning progressed.

Further evidence for automaticity in the ASRT task comes from probing whether participants keep responding according to the old associations they have learned even when those associations are no longer relevant. Szegedi-Hallgató et al.[15] used an experimental design similar to ours but without the Go/No-go manipulation: after participants acquired the associations in an extended learning phase of the ASRT task, the sequence was changed in the rewiring phase, and therefore, some of the acquired associations became less relevant (improbable). The authors tested whether errors committed in the rewiring phase were simple motor control errors or so-called anticipatory errors. While a motor control error could be any incorrect response (i.e., pressing any of the three response buttons that are incorrect for a given stimulus), an anticipatory error would reflect the acquired associative knowledge (i.e., pressing the response button that would be an appropriate response for a high-probability triplet even when participants are presented with a low-probability triplet). They found that participants (in the Implicit-Implicit group that is most closely related to our study) committed anticipatory errors based on the old associations they learned in the previous phase, even though those associations were no longer relevant in the rewiring phase.

Another study by Kóbor et al.[32] introduced a pseudorandom environment (i.e., a stimulus stream lacking any regularities) after the initial extended learning phase of ASRT. They found that the associations learned in the initial learning phase were automatically transferred to and influenced participants' responses in the pseudorandom environment, further highlighting the persistence and automaticity of the acquired knowledge. The introduction of a rewiring phase/pseudorandom environment where the initially acquired associations are no longer relevant could be considered as a test to see whether the presented (sequences of) stimuli automatically elicit responses that were appropriate in the old environment. Therefore, although significant differences exist between these experimental designs in humans and the typical tests (with reinforcers) in animal studies, these designs could shed further light on the automatic nature of the acquired associative knowledge in humans. The results of the present study also

reveal the automatic/persistent nature of the acquired knowledge in that the old knowledge persisted in the irrelevant (new) context when probed in the Testing phase.

As discussed so far, evidence shows that sequence learning tasks, and the ASRT task in particular, can be used to test habit learning in humans as the learning process and the acquired associative knowledge exhibit the behavioral characteristics of habits. Further evidence supporting the use of such tasks comes from studies testing the **neural underpinnings of habits**. It has long been recognized that the striatum (a structure within the basal ganglia) plays a key role in habits[39,40]. Specifically, studies have suggested a shift from reliance on the associative striatum (broadly corresponding to the dorsomedial striatum in rodents) during initial learning to the sensorimotor striatum (broadly corresponding to the dorsolateral striatum in rodents) later in learning[4,40–42]. This has often been interpreted as a shift from a goal-directed to a habitual behavior in animal studies[4].

Learning in the (A)SRT task elicits similar brain activation[41,43]. Specifically, a recent meta-analysis of human functional fMRI data revealed converging activation in the striatum, including the anterior segment of the caudate nucleus and the putamen[41], although this study did not contrast early vs. later phases of learning to test the shift in reliance from the associative to the sensorimotor striatum. In another meta-analysis of functional fMRI data, Lohse et al.[43] tested neural increases and decreases over short, medium and long timescales of a range of tasks that included sequence learning tasks as well. They found increased activation in the putamen over the medium and long timescales, suggesting that an increasing automatization on the behavioral level over extended practice is associated with increased involvement of the putamen (sensorimotor striatum). Finally, another meta-analysis contrasted brain activation during different habit learning tasks directly to test whether the human putamen plays a similar role to the rodent dorsolateral striatum in habitual behavior[13]. They found that outcome devaluation, sequential decision-making, and sequence learning tasks likewise elicited activation in the putamen, suggesting that despite being highly different tasks, they rely on similar learning mechanisms. To sum up, converging evidence from brain imaging studies shows that classic habit learning tasks and implicit sequence learning tasks rely on the same basal-ganglia-based network, both in humans and animals.

In conclusion, we discussed that, compared to habit research in animals, a broader set of behavioral characteristics are used to capture habits in humans. We provided evidence both from previous research and the current study that these characteristics are present in sequence learning tasks, including the ASRT task. Research probing the neural underpinnings of habits

also revealed that the same basal-ganglia-based network is involved in sequence learning and other, more traditional habit learning tasks.

Supplementary results: Reaction times

Raw reaction time (RT) performance

To illustrate how general performance changed throughout the experiment, we present raw RTs in Figure S1.

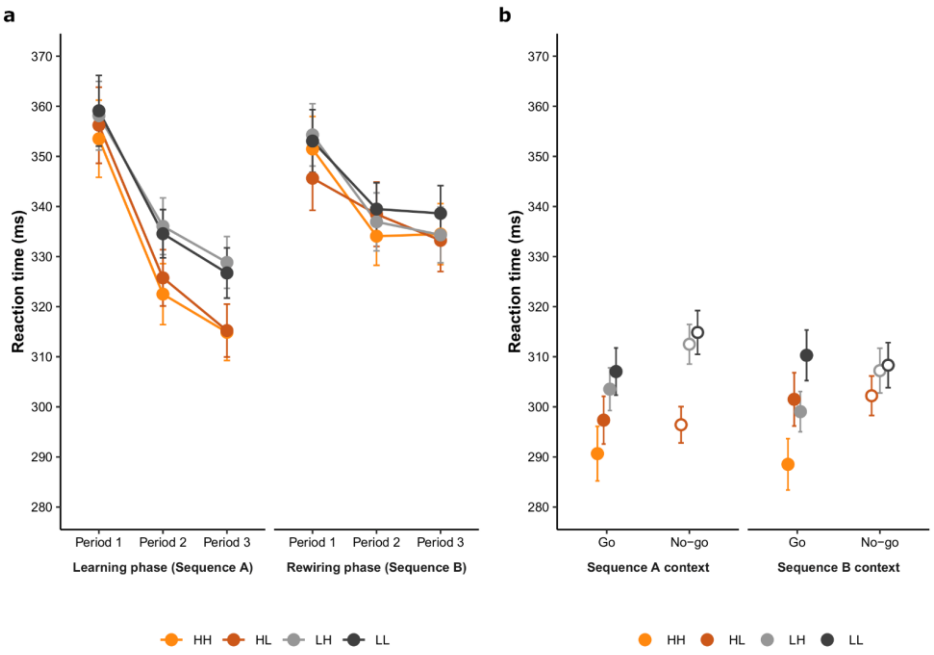


Figure S1. Raw RT performance throughout the experiment. a) Mean RTs measured in the Learning and Rewiring phases, separately for the four trial types (HH, HL, LH, LL). During the Learning phase, RTs were faster for the high-probability trial types (HL, HH) compared with the low-probability ones (LH, LL), indicating acquisition of the associations of Sequence A. In the Rewiring phase, participants showed increasingly faster RTs on the LH trials compared to the LL trials, indicating the acquisition of the Sequence B associations (for detailed analyses, see main text). In these two phases, only responses on Go trials are displayed. b) Mean RTs during the Testing phase, separately for four trial types (HH, HL, LH, LL), the previously Go and No-go trials, and the tested contexts (Sequence A vs. B). Please note that there were no No-go trials within the HH trial type, and therefore the primary measures of interest were derived from the other three trial types (for details see Methods section in the main text). When tested on Sequence A, participants expressed the old knowledge both on the Go and No-go trials (faster RTs for HL than for LL). When tested on Sequence B, the new knowledge was present on the Go (faster RTs for LH than for LL trials) but not on the No-go trials; additionally, the old knowledge (associations of Sequence A) also persisted (faster RTs on HL than on LL) even though it was not relevant in this testing context. The interpretation presented here is supported by analyses on the learning scores reported in the main text. Error bars represent the Standard Error of the Mean (SEM).

How does acquisition of new knowledge compare with the initial learning process?

To answer this question, we directly compared the acquisition of old knowledge in the Learning phase and the acquisition of new knowledge in the Rewiring phase (measured by the 'LL minus HL' and 'LL minus LH' learning scores, respectively). There was no significant difference between the learning trajectories of the old and new knowledge (Phase x Period interaction: $F(1, 30) = 0.657$, $p = .522$, $\eta_p^2 = .021$; circled areas of Figure 3ab), however, the overall magnitude of learning was greater in the Learning than in the Rewiring phase (7.7 ms and 1.9 ms, respectively; significant main effect of Phase: $F(1, 30) = 6.215$, $p = .018$, $\eta_p^2 = .172$). Learning scores gradually increased, irrespective of the phase (main effect of Period: $F(2, 60) = 7.646$, $p = .001$, $\eta_p^2 = .203$). Overall, these results suggest that, although participants were able to acquire the new knowledge, this process was less successful than the initial acquisition of the old knowledge.

Is the level of the new knowledge comparable to that of the old knowledge in the Testing phase?

To test this question, first we performed paired samples t-tests contrasting the old knowledge with the new one in their relevant contexts of the Testing phase (i.e., tested on Sequence A vs. Sequence B, respectively). These data are displayed in the circled areas of Figure 4ab of the main text.

On the Go trials, there was no significant difference between the learning scores ($t(30) = -0.47$, $p = .643$, Cohen's $d = 0.08$, $BF_{01} = 4.715$), suggesting that participants could express both the old and new knowledge in their respective relevant contexts to a similar extent. This finding could be interpreted as flexibility of the acquired knowledge. On the No-go trials, the learning score for the old knowledge was significantly greater than that for the new knowledge ($t(30) = 5.79$, $p < .001$, Cohen's $d = 1.04$, $BF_{01} = 2.841^{e-5}$). Consistent with the finding that only the learning score for the old knowledge was significantly above zero (reported in the main text), this result reveals the detrimental effect of inhibition: on the previously inhibited trials, the old knowledge was reinstated, and the new knowledge was not expressed (and presumably not acquired).

Next, we performed similar analyses to contrast the level of old and new knowledge in the new (Sequence B) context. Thus, data displayed in the non-circled area of Figure 4a and the circled area of Figure 4b of the main text are contrasted in this analysis. On the Go trials, there

was no significant difference between the learning scores (p = .402, Cohen's d = 0.15; BF_{01} = 3.743, indicating strong evidence for no difference), suggesting that participants could express both the old and new knowledge in the new context to a similar extent. On the No-go trials, the learning score for the old knowledge was significantly greater than that for the new knowledge (p < .050, Cohen's d = 0.37, BF_{01} = 0.849). Again, consistent with the finding that only the learning score for the old knowledge was significantly above zero (reported in the main text), this result further supports the detrimental effect of inhibition.

Supplementary results: Accuracy

As it is shown in Figure S2a, there was a ceiling effect in accuracy (97.4% on average) in the Rewiring phase, likely due to the introduction of the Go/No-go manipulation in this phase. Therefore, accuracy data of the Rewiring phase and of the Learning phase for comparability, were analyzed as follows: First, we compared average accuracy measured on the Go trials for the four trial types, separately for the two phases using repeated measures ANOVAs with Trial type (HH, LL, LH, HL) and Period (1, 2, 3) as within-subject factors. Next, we calculated sensitivity indices for the Rewiring Phase only, separately for the LL, LH and HL trial types. For these indices, false alarm rate (on No-go trials) was extracted from the ratio of correct responses (on Go trials). Since all HH trials were Go, these trials could not be included in this analysis. The sensitivity indices were submitted to a repeated measures ANOVA with Trial type (LL, LH, HL) and Period (1, 2, 3) as within-subject factors.

Since participants responded on all trials during the Testing phase, accuracy did not show ceiling effect (91% on average, see Figure S2c), and ANOVAs on learning scores could be performed in accordance with the RT analysis reported in the main text. Learning scores were calculated as follows: for old knowledge, accuracy on LL trials were subtracted from accuracy on HL trials; for new knowledge, accuracy on LL trials were subtracted from accuracy on LH trials. In both cases, higher learning scores indicated better knowledge. Repeated measures ANOVAs with the tested Sequence (Sequence A vs. Sequence B) and Inhibition (Go vs. No-go) as within-subject factors were performed separately for the two learning scores (testing old and new knowledge). Additionally, for comparability with RT analyses, we performed one-sample t-tests to reveal whether the learning scores were significantly above zero.

Greenhouse-Geisser epsilon (ε) correction was used when necessary. Original df values and corrected *p* values (if applicable) are reported together with partial eta-squared (η_p^2) as the measure of effect size. LSD correction was used for pair-wise comparisons to correct for Type I error. We report Cohen's d as a measure of effect size for pairwise comparisons. Additionally, Bayes factors were computed using default JASP priors to see if data provided strong evidence for the results obtained in the frequentist t-tests (anecdotal evidence for the null-hypothesis: $1 < BF_{01} < 3$, at least substantial evidence for the null-hypothesis: $BF_{01} > 3$; anecdotal evidence for the alternative hypothesis: $1 > BF_{01} > 1/3$, at least substantial evidence for the alternative hypothesis: $BF_{01} < 1/3$) [44,45].

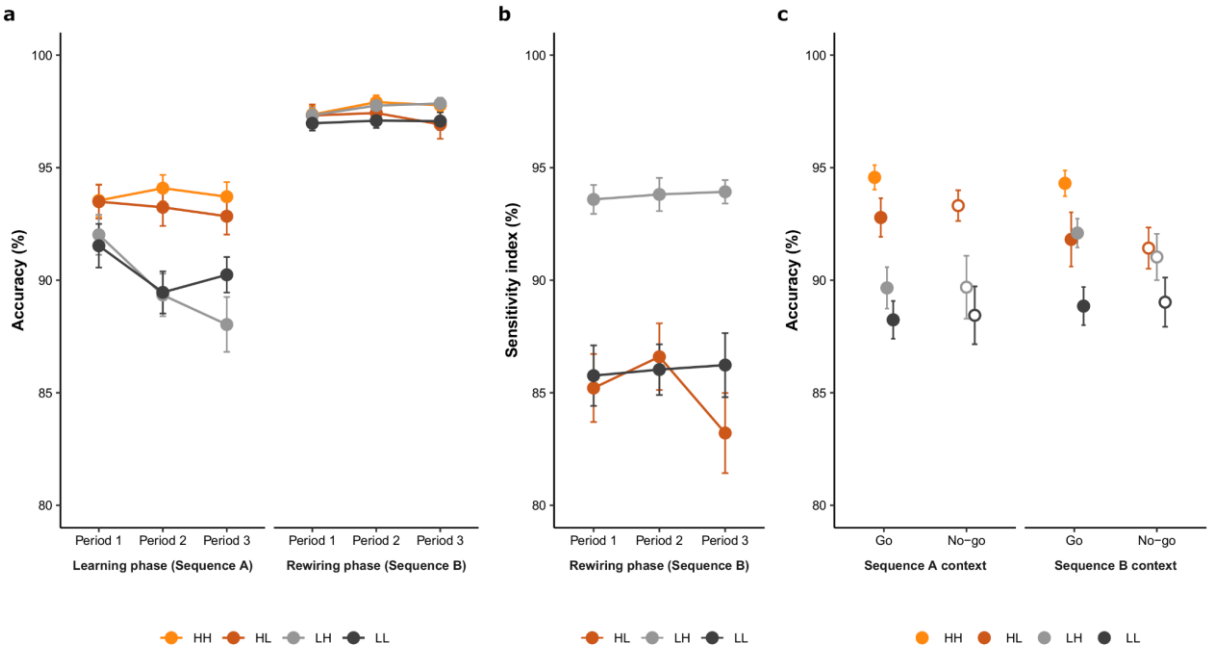


Figure S2. Performance in the Learning and Rewiring phases as measured by accuracy and sensitivity index. (a) The analysis of the Learning phase revealed that participants successfully acquired the associations of Sequence A as there were more accurate on those trials that were high-probability compared to those that were low-probability in this phase (HH and HL vs. LL and LH; underlined letters indicating probabilities of the current comparison; see also Figure 2 in main text). Accuracy in the Rewiring phase was very high due to the introduction of No-go trials, and therefore no significant effects could be detected in the analysis. (b) To track rewiring despite the very high accuracy, sensitivity index (ratio of correct responses minus false alarm rate) was computed for the Rewiring Phase. The analysis of this index revealed that participants successfully acquired the associations of Sequence B as the index was higher (i.e., fewer false alarms) for these trials that became high-probability compared to those that were and/or became low-probability in the Rewiring phase (LH vs. LL, and LH vs. HL, respectively). Additionally, participants showed similar sensitivity index for LL and HL trials, suggesting unlearning of the associations of Sequence A during rewiring. (c) During the Testing phase, participants responded to all trials, and old and new knowledge were tested in both the old (Sequence A) and new (Sequence B) contexts. When tested on Sequence A, participants expressed the old knowledge both on the Go and No-go trials (higher accuracy for HL than for LL). When tested on Sequence B, the new knowledge was also present both on the Go and No-go trials (higher accuracy for LH than for LL trials). Additionally, the old knowledge (associations of Sequence A) also persisted (higher accuracy on HL than on LL) even though it was not relevant in this testing context. The interpretation presented here is supported by analyses on the learning scores reported in the "Results of the Testing phase" section below. Error bars represent the SEM.

Results of the Learning and Rewiring phases. The analysis of the Learning phase revealed that the associations of Sequence A were successfully acquired. Participants were more accurate on those trials that were high-probability in this phase (that is, HH and HL) than on those that were low-probability (LL and LH) (significant main effect of Trial type: $F(3, 90) = 18.956$, p

< .001, η_p^2 = .387), and this difference increased as the task progressed (significant Period x Trial type interaction: $F(6, 180) = 5.718$, $p < .001$, $\eta_p^2 = .160$; Figure S2a). This result suggests that participants successfully acquired the associations of Sequence A. The main effect of Period was also significant ($F(6, 180) = 8.734$, $\varepsilon = .771$, $p = .002$, $\eta_p^2 = .225$) due to the decreasing accuracy on the low-probability trials.

In the analysis of the Rewiring phase, neither the main effects nor the interaction reached significance (main effect of Period: $F(6, 180) = 0.799$, $p = .455$, $\eta_p^2 = .026$; main effect of Trial type: $F(3, 90) = 2.002$, $p = .119$, $\eta_p^2 = .063$; Period x Trial type interaction: $F(6, 180) = 0.571$, $p = .753$, $\eta_p^2 = .019$; Figure S2b), likely due to the very high accuracy on all trial types (97.4% on average).

To track rewiring despite the very high accuracy, we performed an ANOVA using the sensitivity index as described above. The ANOVA revealed a significant main effect of Trial type ($F(2, 60) = 44.178$, $p < .001$, $\eta_p^2 = .596$): the sensitivity index was higher for those trials that became high-probability compared to those that were low-probability throughout the experiment (L<u>H</u> vs. L<u>L</u>: $p < .001$, Cohen's $d = 1.66$, $BF_{01} = 2.471^{e-8}$) as well as compared to those trials that became low-probability in the Rewiring phase only (L<u>H</u> vs. H<u>L</u>: $p < .001$, Cohen's $d = 1.45$, $BF_{01} = 4.415^{e-7}$). This indicates that participants acquired the new knowledge (associations of Sequence B) during the Rewiring phase. At the same time, the latter finding also suggests that unlearning of the old knowledge took place, at least partly, since if participants had responded according to the probabilities of the Learning phase, an opposite pattern would have been expected with higher sensitivity index for the HL than for the LH trials. Moreover, the sensitivity index on those trials that became low-probability only in the Rewiring phase did not differ significantly from that on the trials that were low-probability throughout the experiment (H<u>L</u> vs. L<u>L</u>: $p = .378$, Cohen's $d = 0.16$, $BF_{01} = 3.615$), further suggesting unlearning of the old knowledge (associations of Sequence A). . The main effect of Period and the Period x Trial type interaction did not reach significance ($F(2, 60) = 1, 400$, $p = .254$, $\eta_p^2 = .045$, $F(4, 120) = 2.345$, $p = .059$, $\eta_p^2 = .072$, respectively).

Altogether, these results are consistent with those of RT measures reported in the main text: namely, the associations of Sequence A and Sequence B were both successfully acquired in the Learning and Rewiring phases, respectively, and the associations of Sequence A seemed to be unlearned during the Rewiring phase.

Results of the Testing phase. The ANOVA on the 'HL minus LL' learning score measuring the *old knowledge* (Figure S3a) revealed a significant main effect of Sequence ($F(1, 30) = 6.095$,

p = .129, η_p^2 = .169), with overall smaller learning scores when tested on Sequence B than on Sequence A, suggesting an effect of rewiring. Nevertheless, participants performed above zero in both contexts (p < .001, Cohen's d = 1.18 and p = .006, Cohen's d = 0.53, for Sequence A and Sequence B, respectively), suggesting the persistence of the old knowledge both in the relevant (Sequence A) and irrelevant (Sequence B) testing contexts. The main effect of Inhibition (F(1, 30) = 0.011, p = .915, η_p^2 < .001) and the Sequence x Inhibition interaction did not reach significance (F(1, 30) = 0.277, p = .603, η_p^2 = .009).

In the ANOVA on the 'LH minus LL' learning score measuring the *new knowledge* (Figure S3b), neither of the main effects nor the interaction reached significance (main effect of Sequence: F(1, 30) = 2.442, p = .129, η_p^2 = .075; main effect of Inhibition: F(1, 30) = 0.435, p = .514, η_p^2 = .014; Sequence x Inhibition interaction: F(1, 30) = 0.253, p = .619, η_p^2 = .008). Nevertheless, for comparability with RT analyses, we performed one-sample t-tests to reveal whether any of the learning scores of the new knowledge were significantly above zero. These t-tests revealed that learning scores in the new (Sequence B) testing context were significantly above zero both on the previously Go (p < .001, Cohen's d = 0.86, BF_{01} = 0.002) and No-go trials (p = .043, Cohen's d = 0.38, BF_{01} = 0.756). Opposingly, in the old (Sequence A) testing context, learning scores seemed to be at zero-level both for the No-go trials (p = .397, Cohen's d = 0.15, BF_{01} = 3.717) and Go trials (p = .158, Cohen's d = 0.26, BF_{01} = 2.030).

Overall, the accuracy results of the Testing phase suggest the persistence of old knowledge both in the relevant (Sequence A) and irrelevant (Sequence B) testing contexts, and the simultaneous presence of the new knowledge that was expressed in its relevant (Sequence B) testing context but not in the old (Sequence A) testing context.

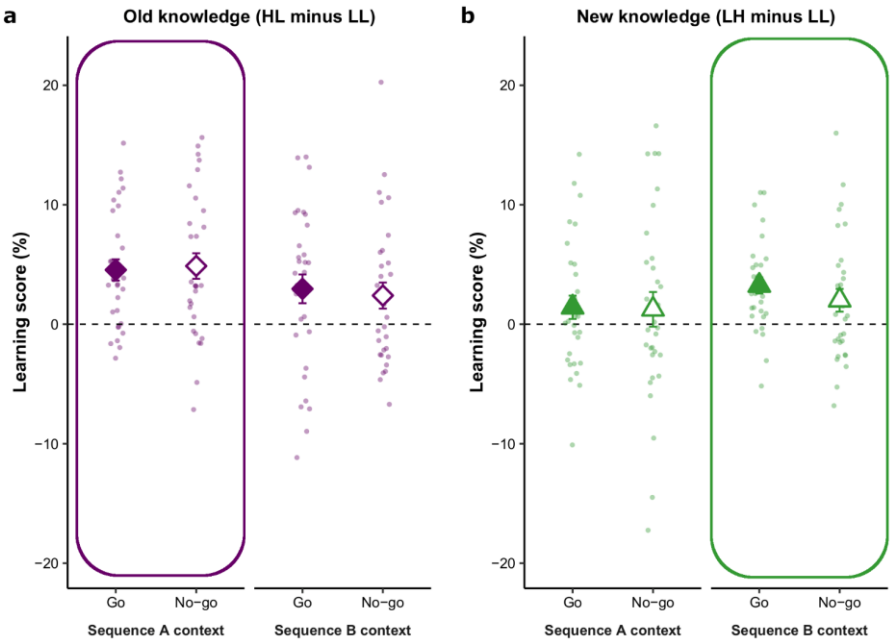


Figure S3. Performance in the Testing phase as measured by accuracy. (a) The analysis of the 'HL minus LL' learning score revealed that the old knowledge was expressed both when tested in the old, relevant context (Sequence A) and in the new context (Sequence B), in which this knowledge was irrelevant. Inhibition of responses during rewiring did not significantly affect these results. (b) The analysis of the 'LH minus LL' learning score revealed that the new knowledge was expressed in the new (Sequence B) context, in which it was relevant, but not in the other context. Again, inhibition of responses during rewiring did not significantly affect these results. Error bars represent the SEM.

Supplementary results: Was the acquired knowledge consciously accessible?

At the end of the Testing phase, a free generation task[15,46] and a triplet sorting task[15,47,48] were administered to probe whether participants acquired consciously accessible knowledge about the probability structure of the task using recall- and recognition-based approaches, respectively.

Free generation task

Task and procedure. In this task, participants were asked to generate a series of responses that followed the order within which stimuli appeared in the ASRT task. The task was administered for Sequence A and Sequence B separately by asking participants to remember what they practiced on Day 1 and on Day 2, respectively, and generate series of responses similar to those that they practiced[46]. This task was used to test if participants could consciously access and control their old and/or new knowledge (associations of Sequence A and B, respectively) to generate responses according to the testing conditions[27,46,49]. The two conditions (Sequence A and B) were administered in a counterbalanced order and each consisted of four runs with 24 button presses. Participants were asked to use the same response buttons as in the ASRT task.

Statistical analysis. To test the performance on the free generation task, first, trials (responses) were categorized as being high- or low-probability both according to Sequence A and Sequence B. This resulted in four trial types (HH, HL, LL, LH), similar to the analyses of the ASRT task. Since three consecutive trials were needed to identify the third trial's probability, 22 trials were evaluated in each run. Second, responses that corresponded to HH or LL triplets were excluded from the analyses because these were the same in Sequence A and B and, therefore, could not be used to probe if participants gained conscious knowledge separately about Sequence A (old knowledge) or Sequence B (new knowledge). Third, the percentage of HL and LH responses out of all evaluated ones (22) were calculated for each run, both for Sequence A and Sequence B. Fourth, we computed averages of these percentages across the four runs in each condition.

HL responses could be interpreted as the knowledge of Sequence A since these reflect high-probability triplets in Sequence A, and LH responses could be interpreted as the knowledge of Sequence B since these reflect high-probability triplets in Sequence B. Therefore, if participants generated more HL than LH responses in the Sequence A condition and/or more LH than HL responses in the Sequence B condition, that would indicate that they gained

consciously accessible knowledge that they could use to control their responses according to the testing conditions[46]. To test this possibility, the percentages of HL vs. LH responses were compared using paired samples t-tests, separately in Sequence A and Sequence B conditions. Additionally, Bayes factors were computed using default JASP priors for all pairwise comparisons[2].

Results. The percentages of HL and LH responses did not differ significantly either in the Sequence A (M_{HL} = 23.70% vs. M_{LH} = 21.20%; $t(30) = 1.176$, $p = .249$, Cohen's $d = 0.21$, $BF_{01} = 5.138$) or Sequence B conditions (M_{HL} = 22.27% vs. M_{LH} = 21.46%; $t(30) = 0.456$, $p = .652$, Cohen's $d = 0.08$, $BF_{01} = 4.210$). This indicates that participants could not consciously control their old or new knowledge to generate their responses according to the testing conditions.

Overall, the results of the free generation task indicate that participants did not gain consciously accessible knowledge either about the associations of Sequence A (old knowledge, tested by HL responses) or Sequence B (new knowledge, tested by LH responses) that they could use to generate their responses according to the testing conditions, thus they remained implicit.

Triplet sorting task

Task and procedure. In this task, participants saw each unique triplet of the practiced sequences and were asked to make forced-choice decisions on their occurrence probability to probe if they gained any consciously accessible knowledge about the learned/rewired associations. The same stimuli were used as in the ASRT task: that is, participants saw a picture with the dog's head appearing in one of the four possible stimulus locations. The three consecutive stimuli that formed a triplet were presented as follows: the first one was presented for 700 ms on the upper third of the screen, then the second one was added to the middle of the screen for another 700 ms. Finally, the third one was also added to the lower third of the screen. All three stimuli remained on the screen until a response was provided. Participants were instructed to remember what they practiced on Day 1 and Day 2, respectively, and decide whether the presented triplet occurred frequently (high-probability triplets) or not (low-probability triplets) for the particular experimental phase (Day 1 vs. Day 2). Thus, all 64 unique triplets were presented to the participants twice: once for determining their probabilities on Day 1 (i.e., in Sequence A) and once for determining their probabilities on Day 2 (i.e., in Sequence B), in a counterbalanced order.

Statistical analysis. To analyze the performance on the triplet sorting task, first we determined correct responses as identifying high-probability triplets as high-probability and low-probability triplets as low-probability separately in the two conditions of the task (i.e., when tested on Sequence A and on Sequence B). Next, we calculated the percentage of correct responses for all four trial types (HH, LL, LH, HL), for both conditions. As in the free generation task, the HL and LH categories were the primary measures of interest. If participants had more correct responses on HL trials in Sequence A than in Sequence B, or vice versa, more correct responses on LH trials in Sequence B than in Sequence A, that would indicate that they gained consciously accessible knowledge about the associations and could successfully identify in which phase of the experiment those associations were more probable.

Since all unique triplets were presented in this task, it enabled us to also categorize triplets based on whether they were inhibited during rewiring or not (i.e., No-go vs. Go trials, respectively) and test the percentage of correct responses as a function of inhibition as well. This resulted in eight measures that were included in the analysis: the percentage of correct responses for HL and LH trials, separately for the previously No-go and Go trials, and separately for Sequence A and Sequence B.

First, we conducted a repeated measures ANOVA on the percentage of correct responses with Trial type (LH vs. HL), Inhibition (Go vs. No-go), and Sequence (tested on Sequence A vs. on Sequence B) as within-subject factors to probe if any of these factors or their interactions affected participants' responses. Finally, all eight measures were tested against chance level (50%) using one-sample t-tests, supplemented by Bayes factors using default JASP priors[2].

Results. The frequentist ANOVA did not reveal any significant main effects or interactions (all ps > .221, all $\eta_p^2 < .05$), suggesting that participants' decisions did not differ as a function of trial type (HL vs. LH), whether they suppressed responses to the tested trials during rewiring (No-go vs. Go), or whether they were tested on Sequence A or on Sequence B.

The percentage of correct responses (ranging from 47.7% to 55.5%) did not differ significantly from chance level (50%) for any of the eight measures (all ps ≥ .280, Cohen's ds ≤ 0.20, BF_{01}s ≥ 3.544 with the exception of LH No-go trials tested on Sequence B where BF_{01} = 2.547), suggesting that participants categorized the triplets as high- or low-probability randomly.

Overall, these results indicate that participants did not gain consciously accessible knowledge about the practiced associations in the experiment, irrespective of the tested

knowledge, inhibition, and testing condition, further reflecting that the acquired knowledge remained implicit.

Supplementary methods

Estimation of required sample size

We calculated the required sample size based on previously published data obtained from the ASRT task. It has been reported that as few as N = 6-7 participants are sufficient to show a significant learning effect with 25 blocks of ASRT at $p = .05$ and power = .80[50,51]. Since in the current study, we used 45 blocks of ASRT, even a smaller sample is expected to be enough to show a significant learning effect.

Nevertheless, as the main focus of the present study was to investigate the rewiring of the acquired knowledge, we conducted further calculations based on the data of Szegedi-Hallgató et al.[15] (Implicit-Implicit group) obtained in a similar task design but without the Go/No-go manipulation using G*Power 3.1[52]. Based on the mean (13.9 ms) and standard deviation (8.59 ms) of the overall learning score of the new knowledge ('LL minus LH') measured over the 45 blocks of the Rewiring phase, the estimated effect size was Cohen's d = 1.62. The required sample size to show this effect at the level of $\alpha = .05$ and with power = .80 is N = 5.

Next, we calculated learning scores corresponding to the old and new knowledge ('LL minus HL' and 'LL minus LH', respectively) measured in their corresponding context (A and B, respectively) in the Testing phase of the same dataset. Accordingly, to show that the old knowledge (M = 12.6 ms, SD = 16.44 ms, Cohen's d = 0.77) was expressed (i.e., was significantly above zero) after rewiring, a sample of N = 12 is needed at $p = .05$ and power = .80. In a similar calculation, we found that to show that the new knowledge (M = 18.2 ms, SD = 17.18 ms, Cohen's d = 1.06) was successfully exhibited in its context, a sample size of N = 8 is required. Importantly, these estimates need to be treated with caution due to the task lacking the Go/No-go manipulation. Consequently, we performed the required sample size analysis with a more stringent criterion as well, expecting a medium effect size (Cohen's d = 0.50) both for the old and new knowledge, with at $p = .05$ and power = .80. This calculation revealed that a sample with N = 27 is required to show significant effects for the old and new knowledge in the Testing phase. Thus, the sample size of our study meets the estimated criteria, including the more stringent one.

Since there is no previous ASRT study with a Go vs. No-go manipulation, for direct comparison of performance on the Go vs. No-go trials within a given context or performance

on Go/No-go trials across contexts, we could not use estimates from previously published studies. However, using the same criteria as above (i.e., expecting a medium effect size of 0.5 with p = .05 and power = .80) we found that N = 27 participants are required to show significantly better performance, for example, on the Go vs. the No-go trials (i.e., one-tailed paired-samples comparison), while allowing significant deviation in either direction (e.g., better performance on Go or on No-go trials, two-tailed comparison) resulted in a required sample size of N = 34. Thus, overall, based on our calculations, a sample size of N = 27-34 would be sufficient for our study. During the recruitment process, we managed to collect data of 33 participants, and the final sample consisted of 31 participants (see Participants section in the main text).

Finally, there are cases where near-zero performance could be expected (e.g., expressing old knowledge in the new context, or vice versa, expressing new knowledge in the old context). Calculating required sample size for these cases would be inappropriate as they would emerge as non-significant results during the analysis. For such non-significant results, Bayes factors could be used to see if there is sufficient evidence for the null-hypothesis (i.e., no difference from zero/non-significant result). At the same time, Bayes factors could also reveal if there is sufficient evidence in the data for the alternative hypothesis. These calculations could be used to confirm/provide further support for the interpretations of significant results. Therefore, we reported Bayes factors where appropriate both for non-significant and significant pair-wise comparisons. For more details on Bayes factors, see the Statistical analysis section in the main text.

Task and procedure

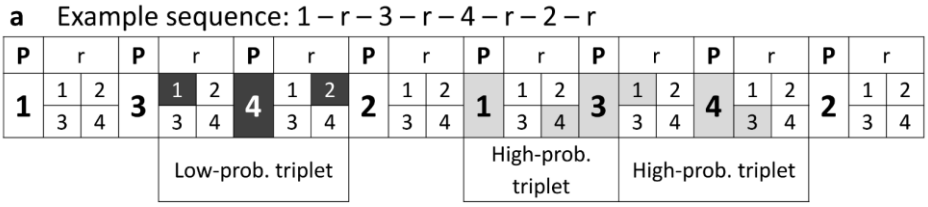
Learning phase. In the ASRT task[22,53], the target stimulus (a dog's head) appeared in one of the four horizontally arranged circles on the screen (see Figure 1 in the main text). Four buttons of a response box (Chronos, Psychology Software Tools) corresponded to the four locations. Participants were asked to press the corresponding button when the stimulus appeared on the screen as fast and as accurately as they could. Unbeknownst to the participants, the stimulus presentation order followed an eight-element sequence, in which predetermined pattern (P) trials alternated with random ones (e.g., 1 – r – 3 – r – 4 – r – 2 – r, where numbers denote the four predetermined locations on the screen from left to right, and *r*s denote the randomly chosen locations out of the possible four).

The task was organized into blocks. One block consisted of 85 trials. In the first five trials, randomly chosen locations were presented and served as a warm-up; this was followed by ten repetitions of the eight-element alternating sequence. Stimuli were presented on the screen until the correct response was provided, followed by a screen with the four empty circles for 120 ms (response-to-stimulus interval, RSI). After each block, participants received feedback about their average RT and accuracy presented for five seconds. If the average accuracy was lower than 80% (irrespective of the average RT), participants were instructed to answer more accurately. If the average accuracy was higher than 95% and the average RT was slower than 250 ms, participants were instructed to answer faster. These settings ensured a good balance between speed and accuracy while encouraging fast responses characteristic of automatic skills and habits[54,55]. After the feedback, a short self-paced break was administered before the next block started. Overall, the Learning phase consisted of 45 blocks (around 45 min), divided into three periods of 15 blocks with five-min breaks in-between to reduce potential fatigue effects[56]. Thus, participants completed 450 repetitions of the sequence (3600 trials, excluding the warm-up trials) in this phase. This extensive practice ensured the acquisition of sound knowledge of the stimulus regularities that has been shown to persist even after a one-year delay (without any further practice)[24,25] and that could serve as a good experimental model for learning processes underlying automatic skills and habits[15,24].

Due to the alternating sequence of stimulus presentation, some runs of three consecutive trials (triplets) were more probable than others. For instance, in the 1 – r – 3 – r – 4 – r – 2 – r sequence, the 1 – x – 3, 3 – x – 4, 4 – x – 2, and 2 – x – 1 triplets (where x denotes the middle element of the triplet) occurred with a greater probability because they were presented in every sequence repetition and could also be formed by chance (see Figure S4). (Notably, since participants were unaware of the alternating regularity, triplets with identical stimuli but with the third element in different (P or r) position were indistinguishable to them[22,53], and responses to them were therefore combined in the analyses.) Meanwhile, for instance, triplets 1 – x – 2 and 4 – x – 3 occurred with a lower probability since they could only be formed by chance. The former triplets are referred to as high-probability triplets, while the latter ones are referred to as low-probability triplets. For all triplets, the third element (*n*) of a triplet was predictable by the first one (*n*-2) of that triplet with a higher or lower probability, while the middle element (*n*-1) did not have a predictive value. Triplets that had the same first and third elements but different middle elements (e.g., 1 – 1 – 3, 1 – 2 – 3, 1 – 3 – 3, and 1 – 4 – 3 for the triplet 1 – x – 3) were therefore treated as identical in all analyses. Importantly, triplets were identified using a moving window throughout the stimulus stream. Thus, *each trial* was categorized as the last element of

a high- or low-probability triplet, and this categorization was used for the RT and accuracy analyses; the same trial then served as the middle and the first element for the categorization of the following triplets.

There were 64 unique triplets in the task, including all pattern-ending (50%) and random-ending (50%) triplets. Sixteen of these unique triplets were of high-probability and 48 triplets were of low-probability. Since high-probability triplets could occur as pattern-ending triplets (50% of all trials) and by chance as random-ending triplets (12.5% of all trials), these triplets constituted 62.5% of all trials in a given session (Figure S4b). Low-probability triplets constituted the remaining 37.5% of the trials; these were all random-ending triplets. Consequently, on the level of unique triplets, high-probability triplets were five times more probable than the low-probability ones (approx. 4% [62.5% / 16] vs. 0.8% [37.5% / 48]). Note that within the low-probability triplets, trills (that is, triplets with the same stimulus as the first and third elements, such as 1 – x – 1), including repetitions (such as 1 – 1 – 1), were excluded from all analyses because participants typically show preexisting response tendencies to them[24,25].



b

	Structure: P – r – P e.g., 1 – r – 3	**Structure: r – P – r** e.g., r – 4 – r
High-probability triplets (62.5% of all trials)	e.g., 1 – 4 – 3 (50%)	e.g., 1 – 4 – 3 (12.5%)
Low-probability triplets (37.5% of all trials)	never occurring (always high)	1 – 4 – 1 (12.5%) 1 – 4 – 2 (12.5%) 1 – 4 – 4 (12.5%)

Figure S4. Stimulus- and probability-structure of the task. (a) Stimulus presentation order followed an eight-element sequence in which predetermined pattern (P) trials alternated with random (r) ones. In the example sequence on the figure, numbers correspond to the four possible locations on the screen from left to right, and the *r*s denote the randomly chosen locations out of the possible four. Due to the alternating sequence structure, some runs of three successive trials (triplets) occurred with a higher probability (light grey) than others (dark grey). These are referred to as high- and low-probability triplets, respectively. For all triplets, the third element (*n*) of a triplet was predictable by the first element (*n*-2) of that triplet with a higher or lower probability, while the middle element (*n*-1) did not have a predictive value. Importantly, triplets were identified using a moving window

throughout the stimulus stream. Thus, *each trial* was categorized as the last element of a high- or low-probability triplet, and this categorization was used for the RT and accuracy analyses; the same trial then served as the middle and the first element for the categorization of the following triplets. (b) Since high-probability triplets could occur as pattern-ending triplets (P – r – P structure; 50% of all trials in a given task session) and by chance as random-ending triplets (r – P – r structure; 12.5% of the trials), these triplets constituted 62.5% of all trials. Low-probability triplets constituted the remaining 37.5% of the trials; these were all random-ending triplets. On the level of unique triplets, high-probability triplets were five times more probable than low-probability triplets.

Rewiring phase. In this phase, a structural change was introduced to the task by replacing Sequence A with Sequence B to prompt the rewiring of old knowledge[15]. Additionally, participants were allowed to respond on some trials (Go trials) but were asked to suppress their response on other trials (No-go trials; see Figure 1 in the main text).

For the Go trials, stimulus was presented until the correct response was provided, followed by a 120 ms RSI. For the No-go trials, stimulus was presented for 1000 ms, followed by a 120 ms delay. In case of a false alarm (i.e., when participants made a response on a No-go trial), the stimulus disappeared from the screen and a warning (a red exclamation mark) was presented for 700 ms, followed by the 120 ms delay. After each block, participants received feedback presented for five seconds. If the average accuracy on the Go trials was lower than 80% (irrespective of the average RT), participants were instructed to answer more accurately. If the average accuracy was higher than 95% and the average RT was slower than 400 ms on the Go trials, participants were instructed to answer faster. Additionally, if participants made more than three false alarms on the No-go trials, they were instructed to follow the instructions more carefully and suppress their responses on these trials. These stimulus timing and feedback settings were determined based on pilot data and were used to ensure that inhibitory control processes were engaged during the No-go trials by providing sufficient time for the activation of the automatic response that then had to be suppressed. The fine-tuned feedback provided a good balance between speed and accuracy; specifically, allowing three false alarms encouraged an overall faster response speed (on the Go trials) to promote rewiring. After the feedback, a short self-paced break was administered before the next block started. As in the Learning phase, the task consisted of 45 blocks (around 45 min), divided into three periods of 15 blocks with five-min breaks in-between. Thus, participants completed 450 repetitions of Sequence B (3600 trials, excluding the warm-up trials) in the Rewiring phase.

Due to the introduction of Sequence B in the Rewiring phase, the probability of some triplets changed: 75% of triplets that were high-probability in the Learning phase became low-probability (HL; thus, the first letter refers to the triplet probability in Sequence A, while the

second letter refers to the probability of the same triplet in Sequence B), and they were replaced by new high-probability triplets that were initially low-probability (LH). Meanwhile, occurrence probability of other triplets remained the same: either being low-probability (LL) or high-probability (HH) in both phases. The HL triplets allowed the assessment of initial acquisition and subsequent unlearning of *old knowledge:* participants could acquire that knowledge in the Learning phase and then had to unlearn it in the Rewiring phase when these triplets become low-probability. The LH triplets allowed the assessment of the acquisition of *new knowledge* as part of the rewiring process: as these triplets became high-probability in the Rewiring phase, knowledge about them could be acquired in this phase. The LL triplets served as a baseline to control for general (i.e., probability-independent) practice and/or fatigue effects (for further details on how the learning scores were calculated see Figure 2b and the Statistical analysis section in the main text). The HH triplets were not used in the analyses; these triplets were included in the design only to have largely but not completely different sequences for the Learning and Rewiring phases as explained above.

An example sequence pair used in the Learning and Rewiring phases is shown on Figure 2a. In this example, the 1 – x – 3 triplets (including all four variations with different middle elements, i.e., 1 – 1 – 3, 1 – 2 – 3, 1 – 3 – 3, and 1 – 4 – 3) were high-probability in both phases (HH). Triplets 3 – x – 4, 4 – x – 2, and 2 – x – 1 (12 triplets overall, including all four variations with different middle elements) were initially high-probability but they became low-probability (HL) because they could occur only by chance (i.e., r – P – r structure) in the Rewiring phase. Triplets 3 – x – 2, 4 – x – 1, and 2 – x – 4 triplets (12 triplets overall, including all four variations with different middle elements) that were initially low-probability became high-probability (LH) because they could occur both as part of the predetermined sequence (P – r – P structure) and by chance (r – P – r structure) in the Rewiring phase. The remaining triplets were low-probability in both phases (LL). We chose sequence pairs that were largely but not completely different for the Learning and Rewiring phases because we believe this resembles everyday examples of changing habit-like behaviors more closely. Specifically, when we try to change our routines (e.g., starting to divide household waste into different bins depending on its material), some steps of the routines may remain unchanged (e.g., still collecting non-recyclable items the same way as before), while other steps need rewiring (e.g., putting items made of glass in a different bin).

The assignment of triplets to Go vs. No-go trials was as follows: Two-thirds of HL triplets were No-go trials (e.g., the 4 – x – 2 and 2 – x – 1 triplets in the above example, including all four variations with different middle elements) to promote the use of inhibitory control

during the unlearning of those triplets that were initially high-probability but then became low-probability in this phase. The remaining one-third of HL triplets were Go trials (e.g., the 3 – x – 4 triplets) to allow comparison of performance later in the Testing phase on those trials that were Go vs. No-go in the Rewiring phase. At the same time, two-thirds of LH triplets were Go trials (e.g., the 2 – x – 4 and 4 – x – 1 triplets in the example above) to promote the acquisition of new knowledge by actively responding on those trials that were initially low-probability and became high-probability in the Rewiring phase. The remaining one-third of LH triplets were No-go trials (e.g., the 3 – x – 2 triplets) for the same reason as above. The assignment of different proportions of HL vs. LH triplets to Go and No-go trials aimed to mimic assumptions about how habit-like behaviors would be rewired in everyday situations, that is, by largely inhibiting the old, unwanted behaviors (more No-go trials on HL triplets) and, at the same time, actively engaging in the new, preferred behaviors (more Go trials on LH triplets). Since performance on LL triplets was used as a baseline throughout the experiment, they were also split into Go and No-go trials following a 2:1 ratio. Finally, as the HH category included only one set of triplets (1 – x – 3 in the example above), they were all Go trials. The ratio of Go and No-go trials across triplet categories was about 50:50 (with some variability due to the randomly chosen locations) to control for general expectation biases.

Overall, eight sequence pairs were selected so that the change in triplet probabilities from the Learning to the Rewiring phase followed the details outlined above. These sequence pairs were used in a counterbalanced order to control for any potential idiosyncrasies in how participants may respond to a particular triplet irrespective of its probability. The allocation of triplets to Go and No-go trials was also counterbalanced across sequence pairs and, therefore, participants. This carefully counterbalanced design ensured that the obtained findings were generalizable across sequences and were not due to pre-existing tendencies on one particular sequence pair.

Testing phase. In this phase, participants performed 20 blocks of the ASRT task (around 20 min) with the same stimulus timing and feedback settings as in the Learning Phase. Unbeknownst to them, knowledge on both Sequence A and Sequence B was tested. In a counterbalanced order, participants completed five blocks containing one sequence (A or B), then five blocks containing the other sequence (B or A), then the whole procedure was repeated once more, resulting in altogether ten-ten task blocks with each sequence (in ABAB or BABA order; see Figure 1 in the main text). Participants responded on all trials, including the ones that were No-go in the Rewiring phase. This enabled the testing of how inhibitory control affected

(un)learning processes during rewiring. After completing the ASRT task, participants were debriefed and informed that the stimuli followed a predetermined order in the task. Then, a free generation task and a triplet sorting task were administered to probe whether participants acquired consciously accessible knowledge about the sequence and/or probability structure of the task (for details, see section ‘Supplementary results: Was the acquired knowledge consciously accessible?’).

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APPENDIX V: THE RESULTS OBTAINED IN THE CORRELATIONAL ANALYSES OF STUDY 1-4.

Table 1. Association between procedural learning ability and the performance on various neuropsychological tests in Study 1-4.

		Study 1 (N = 24)	**Study 2** (N_S = 25, N_U = 25)				**Study 3** (N_C = 48, N_U = 48)				**Study 4** (N = 30)		
		Procedural learning[1]											
		Maximized learning	Triplet learning (TL)		TL updating		Statistical learning (SL)		SL expression		TL	TL rewiring	
			Structured-first group	Unstructured-first group	Structured-first group	Unstructured-first group	Cued group	Uncued group	Cued group	Uncued group		Old	New
		r	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*
Executive control system[2]	Orienting attention	–	–	–	–	–	< .001	.189	-.130	.133	.326	.344	.092
	Alerting attention	–	–	–	–	–	.057#	-.090	.314#	-.120	.294	-.311	-.191
	Interference suppression	–	–	–	–	–	-.130#	-.130#	.071#	.169#	-.158	.082	-.148
	Response inhibition	–	.035	-.080	-.032	-.043	–	–	–	–	-.345	.245	.151
	Updating	.218	.010	.054	-.068	-.030	.136#	.011	.196#	-.004	.082	-.155	.068
	Shifting	-.672#*	-.061	-.185	.037	.202	–	–	–	–	-.242	.009	.076
Short-term memory		-.119	–	–	–	–	-.120#	.030#	-.060#	.147#	.101#	.103#	.144#

Note. * $p < .05$; *r*: Pearson's correlation coefficient; # due to the violation of normality, Spearman's rank correlation coefficient is presented. To control for Type I errors, FDR correction was applied to all tests. [1]Aspects of procedural learning were measured slightly differently in each study, for more details, see the corresponding article. The updating score of Study 2 was calculated as the difference between performance showed at the end of the structured half and at the end of the unstructured half. The rewiring score of Study 4 was calculated as the difference between knowledge expressed on the corresponding and opposite contexts (sequence), separately for the old and the new knowledge, only on the Go trials. [2]Components of the executive control system were measured by the following tasks: the orienting attention, alerting attention, and interference suppression were assessed by the Attention Network Test (Fan et al., 2002); response inhibition was assessed by the Go/No-go task (Gordon & Caramazza, 1982); updating was assessed by the Counting Span task (Case et al., 1982); and shifting was assessed by the Wisconsin Card Sorting Test (Berg, 1947). Short-term memory was measured by the Digit Span task (Isaacs & Vargha-Khadem, 1989). Where no correlation coefficient is indicated in the table, the given neuropsychological test was not assessed. None of these tests were administered in the Supplementary Study.