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FACULTY OF EDUCATION AND PSYCHOLOGY

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

Theses of the doctoral dissertation

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List of publications used in the dissertation

- I. **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>
- II. 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>
- III. **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>
- IV. **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>
- V. **Horváth, K.**, Kardos, Z., Takács, Á., Nemeth, D., Janacsek, K., & Kóbor, A. Manipulation of inhibitory control does not influence procedural learning. *Under construction*.

List of publications (directly) not used in the dissertation

- Bastos, PM Amalia*, **Horváth, K.***, Webb, L. Jonathan, Wood, Patrick M., Taylor, Alex H. (2021). Self-care tooling innovation in a disabled kea (*Nestor Notabilis*). *Scientific Reports*, 11(1), 18035. <https://doi.org/10.1038/s41598-021-97086-w> *Shared first authorship.
- Takács, Á., Kóbor, A., Kardos, Z., Janacsek, K., **Horváth, K.**, Beste, C., Nemeth, D. (2021). Neurophysiological and functional neuroanatomical coding of statistical and deterministic rule information during sequence learning. *Human Brain Mapping*, 42(10), 3182-3201. <https://doi.org/10.1002/hbm.25427>
- Kóbor, A., Kardos, Z., **Horváth, K.**, Janacsek, K., Takács, Á., Csépe, V., Nemeth, D. (2021). Implicit anticipation of probabilistic regularities: Larger CNV emerges for unpredictable events. *Neuropsychologia*, 107826. <https://doi.org/10.1016/j.neuropsychologia.2021.107826>

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- Simor, P., Zavecz, Zs., **Horváth, K.**, Éltető, N., Török, Cs., Pesthy, O., Gombos, F., Janacsek, K., Nemeth, D. (2019). Deconstructing Procedural Memory: Deconstructing Procedural Memory: Different Learning Trajectories and Consolidation of Sequence and Statistical Learning. *Frontiers in Psychology*, 9, 2708. <https://doi.org/10.3389/fpsyg.2018.02708>
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I. Background and aims of the dissertation

Automatic and goal-directed actions are both essential for smoothly adapting our behaviour according to the environment and our own goals. Automatic behaviours, such as habits and skills, at least partially rely on the procedural memory system (Ashby & Crossley, 2012; Ullman, 2001). Acquisition and memory expression in the procedural memory system are implicit, incidental, and automatic (Foerde, 2018; Graybiel, 2008; Henke, 2010), and the acquired automatic behaviours seem highly robust and resistant to forgetting and memory interference (Kóbor et al., 2017; Romano et al., 2010).

In the dissertation, the procedural memory system was assessed by the Alternating Serial Reaction Time (ASRT) task (Howard & Howard, 1997), which is a four-choice reaction time task containing a repeating regularity, unbeknownst to the participants. Within the repeating regularity, predefined pattern trials alternate with randomly selected ones. Due to this alternating nature of the stimulus stream, some events of consecutive trials appear with a greater probability as they are presented in every repetition of the sequence (probable events). However, probable events can also appear by chance consisting of two random trials and one pattern trial as the middle element (probable, but random events). On the other hand, there are some events appearing with a lower probability as they can be formed by chance only (improbable events). Probable events, through practice, can be learnt and predicted, whereas improbable events remain unpredictable. By contrasting performance on the different events as well as by applying the proper experimental manipulations, various aspects of the procedural memory system can be assessed in the ASRT task, such as sequence learning, statistical learning, or habit learning.

Goal-directed behaviours rely on a complex ensemble of various cognitive processes that operate in an orchestrated manner (Friedman & Robbins, 2022). In my dissertation, I refer to this ensemble of cognitive processes as the “executive control system” and conceptualize them according to Bari and Robbins (2013). In their framework, attention and inhibition are identified as core components, while performance monitoring continuously supports these processes. When performance is suboptimal, the auxiliary processes of shifting, selecting, and updating are activated.

Procedural memory and the executive control system frequently need to operate simultaneously during behaviour adaptation. Yet, the exact neurocognitive background of their interplay is still unclear. 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; Poldrack & Packard, 2003), whereas others proposed an independent relationship (Jiménez et al., 2020) between the two systems.

The present dissertation aims to unravel some of the questionable points in the literature in a series of five studies. To this end, I have set out to systematically probe the interplay between procedural memory and the executive control system in a way that the different aspects and phases of learning and the different executive control components are considered. Study 1 and Study 2 investigated the interplay without manipulating either process, whereas Study 3, Study 4 and the Supplementary Study involved the experimental manipulation of the executive control system.

II. New scientific results

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

Thesis I. Electrophysiological and behavioural correlates of error processing are sensitive to general task adaptation processes but not procedural learning and memory retrieval.

A key component of the executive control system is performance monitoring, especially the processing of erroneous actions. The automatic detection that an error has occurred can be tracked by the error-related negativity (ERN, or error negativity, Ne; Falkenstein et al., 1991; Gehring et al., 2012) event-related brain potential (ERP) component, whereas the conscious evaluation of errors is linked to the error positivity (Pe; Falkenstein et al., 1991; Nieuwenhuis et al., 2001). On the behavioural level, the most prominent correlate of error-driven adaptation can be detected by the post-error slowing effect (PES; Egner, 2014), i.e., the slow down following errors. In this study, error-processing were measured during acquisition and retrieval of an automatic behaviour. Participants (N = 24 healthy young adults) completed 30 blocks of the cued ASRT task (Kóbor et al., 2018), where the repeating pattern trials are indicated with a different stimulus and participants are instructed to memorise their order. Subsequently, this information could have been potentially retrieved to achieve better task performance.

A sequence report task administered after every task block showed that the acquisition of the order information successfully took place at the very beginning of the task (Figure 1). A further performance increase on the repeating cued pattern trials suggested the retrieval of this information. The analysis of the ERP data revealed a decreasing Ne, irrespective of trial type, suggesting a drop in error significance. The Pe was increasing over time likewise irrespective of trial type (Figure 2), suggesting that error awareness was increasing. Analysis of the PES effect revealed that participants indeed slowed down after an error has occurred, and this effect decreased as the task progressed similarly for pattern and random trials.

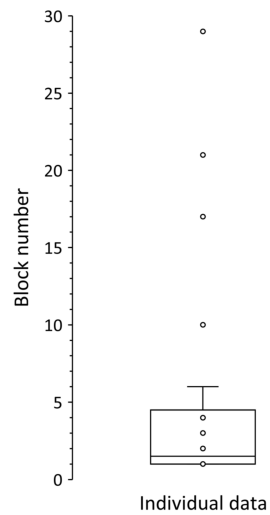


Figure 1. Discovery of the order of the repeating cued pattern trials according to the post-block sequence report task. On average, participants discovered the sequence order within the first five blocks.

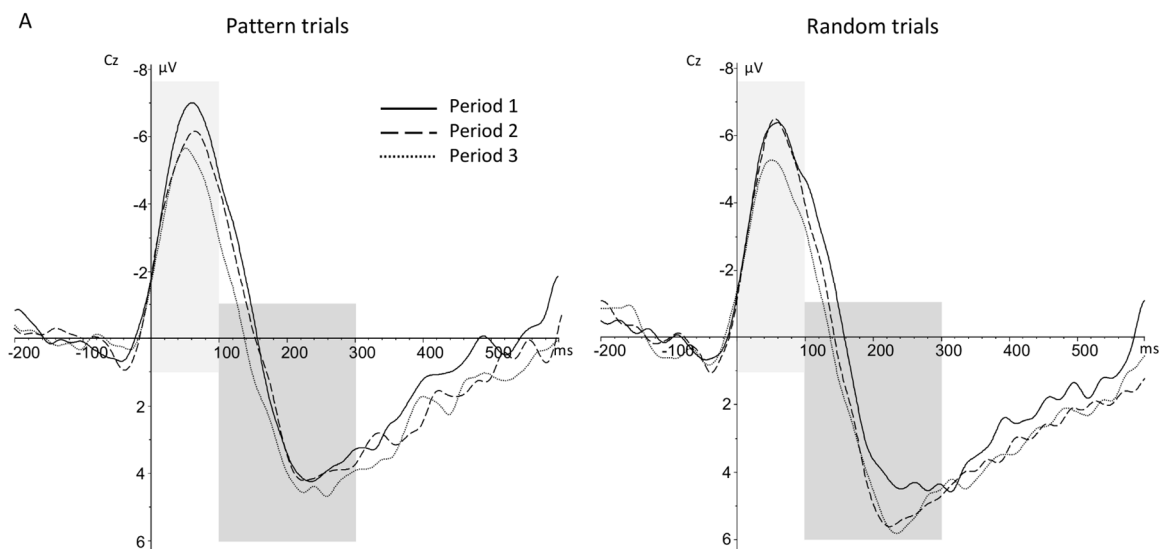


Figure 2. Error minus correct response-locked ERP waveforms at electrode Cz, displaying the Ne (0-100 ms, light grey shading) and the Pe (100-300 ms, dark grey shading) separately for pattern trials and random ones over three time units (10 task blocks each). While the Ne decreased over time, the Pe increased. Neither component showed any retrieval-specific effects but rather a general adaptation to the task.

Overall, Study 1 showed that when an automatic behaviour can be retrieved to achieve better task performance, error processing reflects general task adaptation processes instead of retrieval-specific effects both at the electrophysiological and behavioural levels. Based on Study 1, aspects of procedural memory and performance monitoring have an independent relationship during behaviour adaptation.

ii. 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?

***Thesis II.** Automatic behaviours are persistent and can contribute to behaviour adaptation even in an unpredictable environment. Behaviour adjustment takes longer than initially developing the behaviour.*

An important aspect of the procedural memory system are habits and habit-like automatic behaviours. To successfully adjust habits, the involvement of the executive control system is often required, or, alternatively, habits may adjust without conscious effort when changes in the environment forces them (Robbins & Costa, 2017; Wood & Neal, 2007). However, changing habits is challenging as the old behaviour seems to be hard to break (Poldrack, 2021).

Study 2 aimed to test if and how we can adjust habit-like automatic behaviours when the environment becomes unpredictable without any noticeable change at the surface level in a between-groups experimental design. 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), that was unpredictable. As a control, another group completed the two task parts in a reversed order, thus acquisition of an automatic behaviour took place following experience with the unpredictable environment here. Crucially, the change in the underlying structure was always unsignaled (i.e., participants were not informed about it).

According to the results, the prior automatic behaviour was persistent and exhibited even in the new, unpredictable environment. Over exposure to the unpredictable environment, however, this behaviour was updated accordingly. Crucially, the updating process took longer than initial learning (Figures 3a and 3b). The control group successfully acquired the automatic behaviour even following exposure to the unpredictable environment (Figures 3c and 3d).

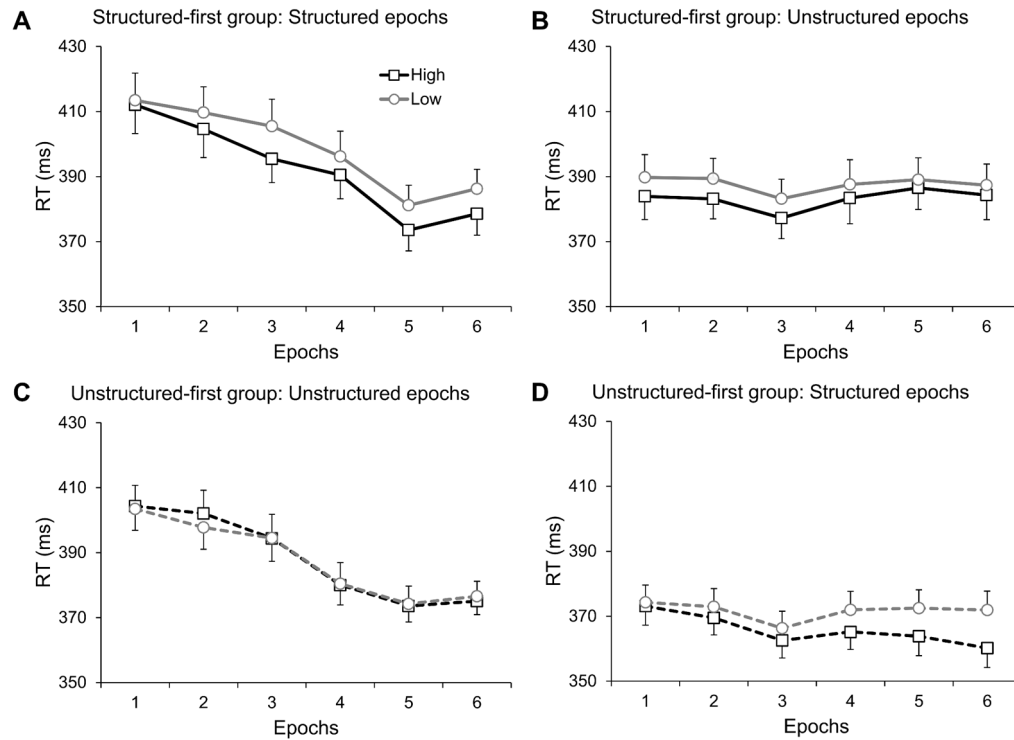


Figure 3. Performance of the two groups (upper and lower rows) over the predictable/structured task part (A and D) and the unpredictable/unstructured task half (B and C), as a function of time. The group completing the predictable part first successfully acquired a habit-like automatic behaviour, which then persisted and was expressed in the unpredictable environment. The behaviour was updated over time. The control group showed no learning in the unpredictable environment, and subsequently acquired the habit-like automatic behaviour in the predictable environment. Error bars represent the standard error of the mean.

Based on Study 2, automatic behaviour adjustment and adaptation can successfully take place even if changes in the environment are hidden. However, this study did not focus on and thus could not directly test the procedural memory vs. executive control system interplay during behaviour adaptation. Goal-directed updating processes might have been intentionally or spontaneously activated in the task, but it is not possible to confirm or deny this presumption in the present experimental design.

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

Thesis III. Dividing attention between concurrent tasks has no impact on the acquisition and retention of automatic behaviours.

Attention is one of the two core components of the executive control system (Bari & Robbins, 2013). Among its numerous and various aspects, divided attention refers to the ability to simultaneously divide attention and keep focus on at least two concurrent tasks or task goals, and it is linked to the executive network of attention (Fernandez-Duque & Posner, 2001; Jiménez & Mendez, 1999).

In this between-groups design study, a divided attention manipulation was introduced during the acquisition of an automatic behaviour. Half of the participants (N = 48) completed a fast and fixed-paced version of the cued ASRT task. Due to the timing manipulation together with the sequence cueing, this group had two concurrent task goals: maintaining good performance and intentionally memorise the order of the cued repeating pattern trials (Learning phase). The other half (N = 48) completed a similarly modified version of the original (uncued) ASRT task without a secondary task, serving as a control. In addition, performance was tested following a 12-hr offline delay to assess another crucial aspect of procedural memory: the retention of the acquired behaviour (Testing phase).

According to the sequence report task administered following each task block in the group completing the cued task version, the timing manipulation hindered the acquisition of the repeating sequence order (Figure 4), suggesting that attention had to be divided. Procedural learning was measured on improbable/unpredictable random and probable/predictable, but random events of the ASRT regularity. The two groups showed a similar level of (incidental) procedural learning, and the acquired behaviour was retained over the offline delay, similarly across the groups (Figure 5).

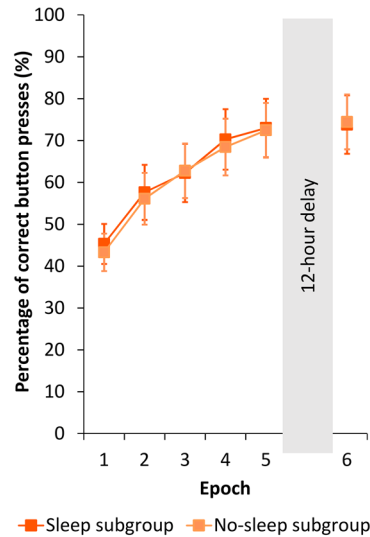


Figure 4. Performance of the divided attention group on the post-block sequence report task as a function of time (Learning phase: epoch 1-5, Testing phase: epoch 6). Although improved over time, participants never reached perfect performance as opposed to results from the cued ASRT task with standard timing settings where the discovery of the sequence happens usually within the first five blocks (Horváth et al., 2021; Kóbor et al., 2018). The group was further divided into two subgroups based on their activity during the offline delay (sleep or awake activity) which is irrelevant from the viewpoint of the dissertation. Error bars represent the standard error of the mean.

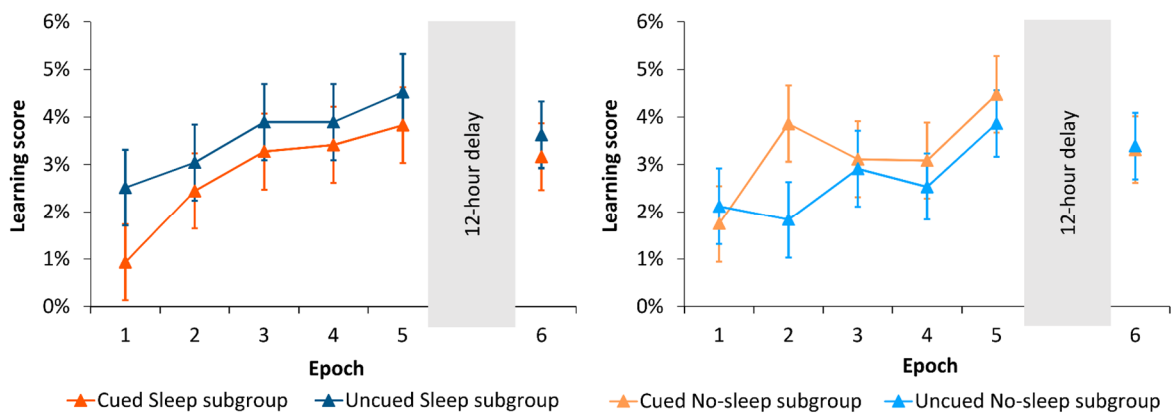


Figure 5. Learning scores calculated from standardized reaction time data as a function of time (Learning phase: epoch 1-5, Testing phase: epoch 6). Yellow lines represent the group performing under the divided attention manipulation and blue lines represent the control group. The groups were further divided into four subgroups based on their activity during the offline delay (sleep or awake activity) which is irrelevant from the viewpoint of the dissertation.

Procedural learning was similar across the groups during the Learning phase and following the 12-hr delay. The acquired behaviour was retained during the offline period. Error bars represent the standard error of the mean.

To sum up Study 3, divided attention did not influence the procedural memory system, but the two processes had an independent relationship.

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

Thesis IV. Response inhibition disrupts the acquisition and the unlearning of habit-like behaviours. Procedural learning may support response inhibition.

Besides attention, inhibition is identified as a core component of the executive control system (Bari & Robbins, 2013), and it encompasses response inhibition and interference suppression (Bryce et al., 2011; Luk et al., 2010). Study 4 investigated the effect of response inhibition, a common naïve response for stopping unwanted behaviours, on changing habit-like automatic behaviours. So far, it has been shown that extinction, an experimental manipulation similar to a response inhibition manipulation, cannot successfully erase habit-like behaviours (Bouton, 2019), and the old behaviour tends to remain present even following a rewiring-like updating procedure (Szegedi-Hallgató et al., 2017).

In this within-subject design study, first, participants ($N = 31$) acquired a habit-like automatic behaviour over extended practice in the original, fully implicit version of the ASRT task. Then, following a 24-hr offline delay, this behaviour was challenged in two ways. On the one hand, a new but partially overlapping regularity was introduced in the task in order to rewire the so-called old behaviour. The partial overlap enabled the simultaneous testing of unlearning the old and acquiring the new behaviour. On the other hand, the response inhibition was engaged in the task in the form of a Go/No-go task-like manipulation. Following another 24-hr offline delay, both the old and new behaviours were tested as well as the effect of response inhibition on both.

According to the findings, the old behaviour was somewhat unlearned, and the new behaviour was successfully acquired during the rewiring procedure. Interestingly, the sensitivity index, i.e., the difference between correct response rate on the Go events and false

alarm rate on the No-go events of the task, revealed that response inhibition was somewhat supported by acquisition of the new behaviour. As shown by the results from the third experimental session, the old behaviour survived the rewiring manipulation, and response inhibitions strengthened it even more (Figure 6a). The new behaviour was also retained, though it appeared weaker than the old (Figure 6b). Response inhibition had a detrimental effect on both unlearning the old behaviour and acquiring the new.

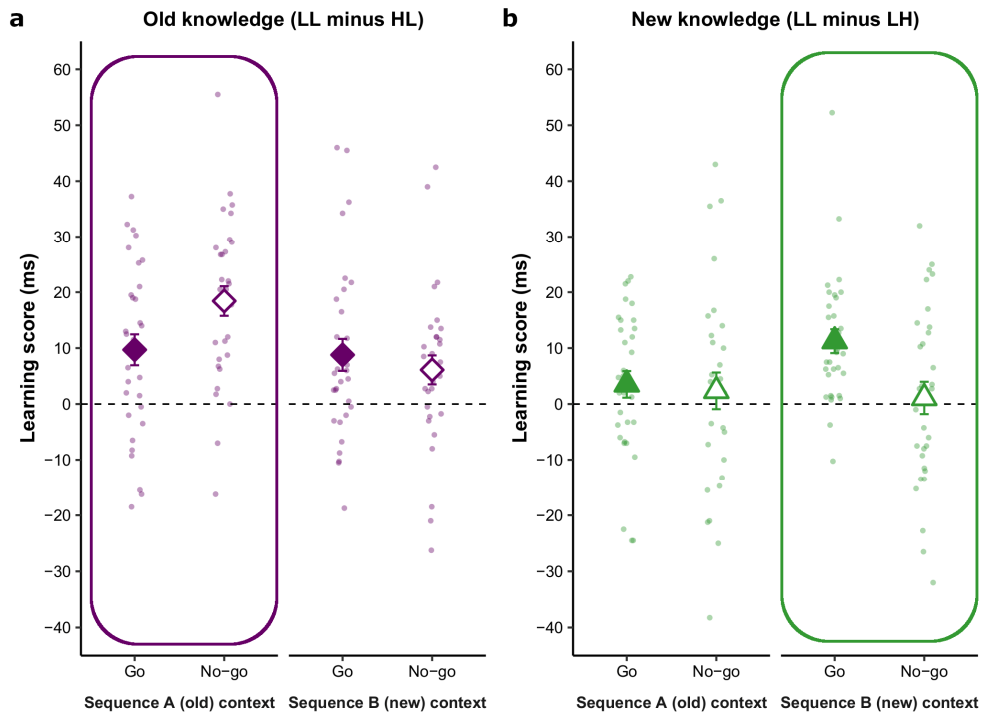


Figure 6. Learning scores obtained in the testing phase, i.e., the third experimental session. Context refers to the underlying regularity of the first day (A; old behaviour) and the second day (B; new behaviour). ‘Go’ refers to those parts of both the old and the new behaviour that were responded during the rewiring procedure, whereas ‘No-go’ refers to those parts that had to be inhibited. a) The old behaviour survived the rewiring manipulation, it was expressed in the context of the new behaviour as well and was further strengthened by the response inhibition manipulation. b) The new behaviour was retained as well, but was expressed only in its corresponding context, and the response inhibition manipulation disrupted the behaviour. Dots represent individual data and error bars denote the standard error of the mean.

Based on Study 4, response inhibition and habit change have a competitive relationship; however, some evidence emerged for the support of response inhibition by the procedural learning processes.

v. Supplementary Study: How do procedural learning and interference suppression influence one another when simultaneously involved in fulfilling task goals?

Thesis V. Interference suppression and the acquisition of automatic behaviours operate independently but may interact under increased environmental uncertainty and conflict.

Interference suppression refers to the filtering of distracting information that interferes with the task goals (Luk et al., 2010). In the Supplementary Study, the Eriksen flanker task (Eriksen & Eriksen, 1974), one of the most prominent experimental paradigms to measure interference suppression was introduced during the acquisition of an automatic behaviour. By doing so, testing the interaction of interference suppression and procedural learning was enabled, in a way that the underlying sequence did not predict/correlate with the distractor stimuli. In addition, the congruency sequence effect (CSE), a conflict-driven behavioural adjustment process was considered. The CSE refers to the phenomenon that the flanker congruency effect is reduced following an incongruent trial than a congruent one as it becomes less demanding (Egner, 2007).

In this within-subjects design study, participants ($N = 36$) completed the fully implicit version of the ASRT task while neutral, congruent, or incongruent flanker stimuli were presented alongside the target stimulus. According to the main analysis, both procedural learning and interference suppression operated independently in the task: learning was similar across all flanker congruency conditions and the flanker congruency effect was comparable on the improbable/unpredictable random and the probable/predictable, but random trials of the ASRT regularity (Figure 7). Surprisingly, the flanker congruency effect generally decreased over time, suggesting that procedural learning might have supported interference suppression at some level. However, the analysis of the CSE suggested interaction between the two processes: the adaptation effect was present in the case of improbable/unpredictable events only (Figure 8). Finally, a correlational analysis of the relationship between procedural learning performance and interference suppression performance revealed that 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.

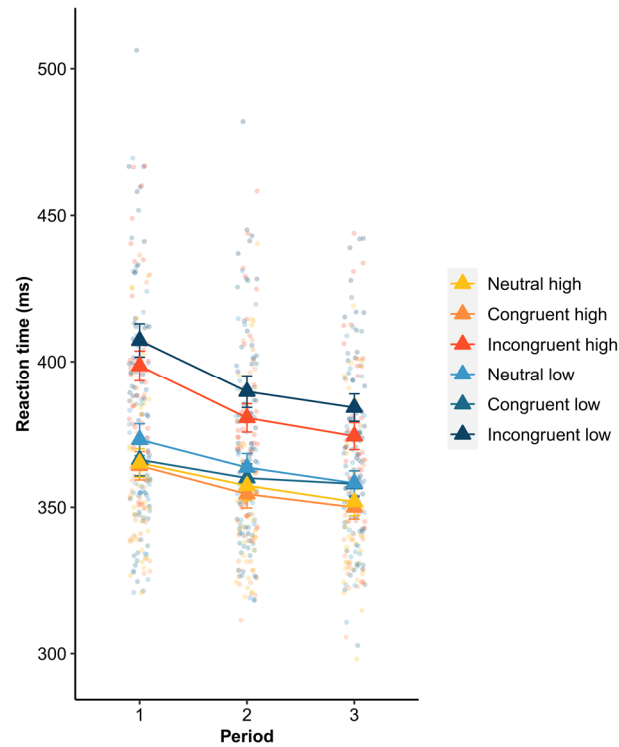


Figure 7. Main task performance measured by RTs over the course of the task. Blue colours represent performance on the improbable/unpredictable ASRT events and orange colours represent performance on the probable/predictable ones. Congruency is indicated by colour gradient, from lightest to darkest respectively for neutral, congruent, and incongruent trials. Participants performed better on the probable/predictable events compared with the improbable/unpredictable events, indicating successful procedural learning. Learning was similar across all flanker congruency conditions. Flanker congruency effect was indicated by better performance on the neutral and congruent conditions compared with the incongruent condition and was comparable between the high-probability/predictable and low-probability/unpredictable events. Dots represent show individual data points. Error bars represent the standard error of the mean.

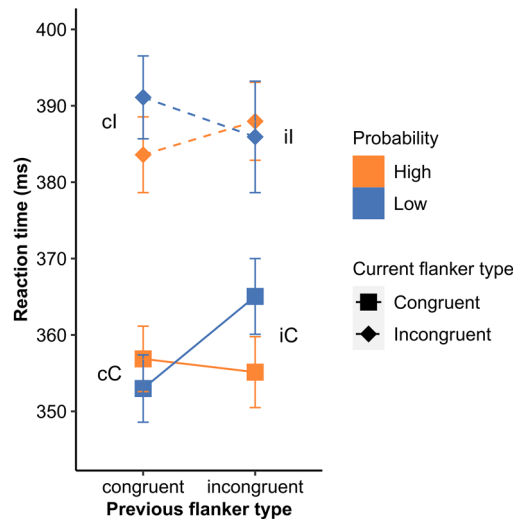


Figure 8. Congruency sequence effect. Blue represents performance the on unpredictable/improbable events and orange represents performance on the probable/predictable. Current trial congruency is indicated by different shapes and lines and capital letters: congruent trials are represented by squares, 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 CSE was apparent on the improbable/unpredictable events only. Error bars represent the standard error of the mean.

Based on the Supplementary Study, procedural learning and interference suppression have a mixed relationship. While both processes were intact and seemed to be operating independently, when conflict and uncertainty were both high in the task, some evidence for their interference emerged.

III. Conclusions

In this dissertation, I presented five studies aiming to gain insight into the nature of the procedural memory vs. executive control system interplay during behaviour adaptation. The main findings are summarised in Figure 9.

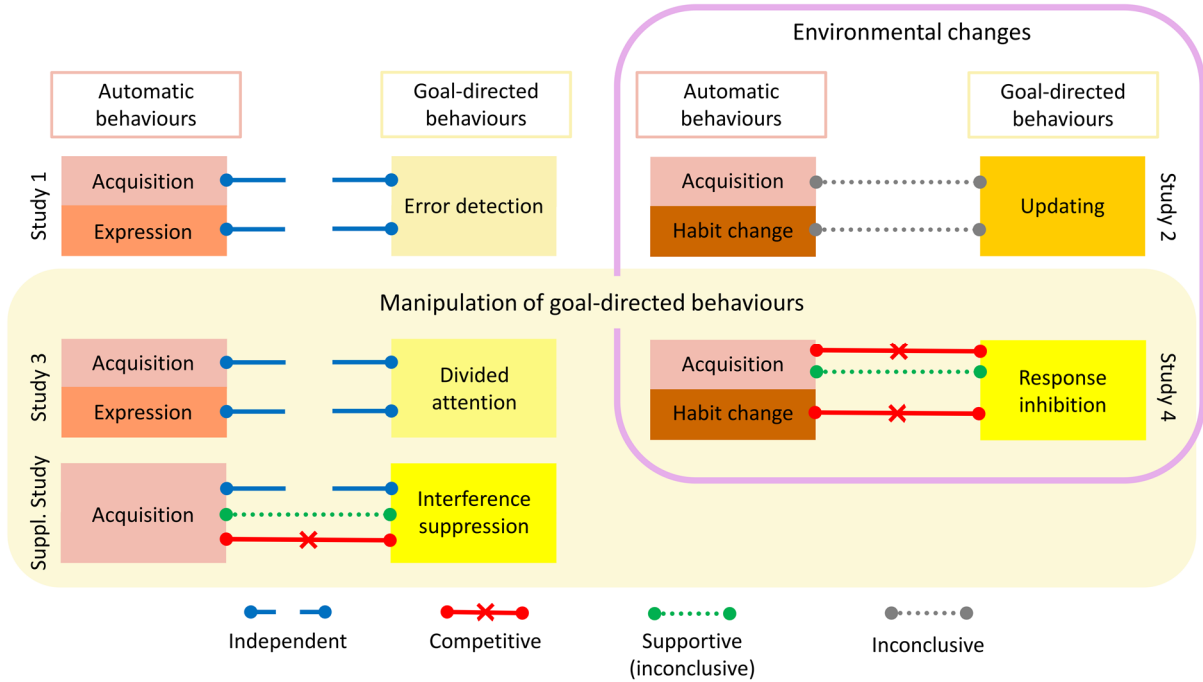


Figure 9. Summary of main findings and theses. Study 1 and Study 2 investigated the procedural memory vs. executive control system interplay during behaviour adaptation without manipulating either. Study 3, Study 4, and the Supplementary Study involved the experimental manipulation of the executive control 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. 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.

Based on the results presented in the dissertation, a converging pattern emerged. While an independent relationship was found when studying acquisition (Study 1, Study 3), competition/interference was revealed in more fragile and complex situations, like habit change

and conflict-driven adaptation (Study 4, Supplementary Study). 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. Thus, the interplay of these two systems may vary across different phases of procedural memory and/or across the processes contributing to the executive control system and could be characterized by an independent or a competitive nature accordingly. On the other hand, when investigated from the viewpoint of the executive control system, some evidence for a supportive relationship emerged (Study 4, Supplementary Study), nevertheless these results remained inconclusive 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.

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, 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 unravelling the interplay of automatic and goal-directed behaviours, and thereby develop methods to improve behaviour adaptation in our everyday life.

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