Age-related Differences in Implicit Sequence Learning and Consolidation across the Human Life Span: Implications for the Functioning of the Fronto-Striatal Circuitry

Summary of PhD Thesis

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Summary

Implicit sequence learning occurs when information is acquired from an environment of complex stimuli without conscious access either to what was learned or to the fact that learning occurred. In everyday life, this learning mechanism is crucial for adapting to the environment and for predicting events unconsciously. Despite the growing interest in implicit learning in the past decades, there has been relatively little research on life-long development of implicit sequence learning and on offline processing of implicitly learned information (i.e., consolidation). Here, we present three studies investigating these issues. In Experiment I, we investigated implicit sequence learning from 4 to 85 years of age and found a marked decrease in learning performance - measured by raw reaction time (RT) – around age of 12. This decrement can be explained by a competition between two fundamentally different forms of learning (model-free and model-based) suggesting that after adolescence frontal lobe-mediated model-based learning has larger effect on the expression of implicit sequence knowledge, while before adolescence basal ganglia-dependent model-free learning is more influencing. As a growing body of data has shown that frontal lobe-mediated processes are disrupted in hypnosis, we tested this assumption in Experiment II by comparing implicit sequence learning in hypnosis and in waking alert state. We found that hypnosis boosted sequence learning in young adults. In addition, this boosting effect was mediated by frontal lobe related executive functions. Finally, we investigated consolidation of implicit sequence knowledge in young and elderly adults after 12-, 24-hour or a 1-week delay period in order to determine age-related differences not only in online learning, but also in offline processing of the learned material (Experiment III). We found that consolidation is not a single process, rather there are multiple mechanisms (e.g., sequence-specific, general skill learning) which are differentially affected by aging and the course of time. Our results contribute not only to the better understanding of learning on a behavioral level, but also to understanding the age-related changes in brain plasticity in healthy participants across the human life span. In addition, these findings can help better understand neurodevelopmental (e.g., autism, dyslexia), neurodegenerative (e.g., Parkinson's Disease, Huntington's Disease) and age-related disorders where related brain structures are affected. Finally, our findings can lead to the development of more effective diagnostic tools, training methods and rehabilitation programs.

Introduction

Prediction is one of the most fundamental functions of the brain. In order to recognize time-based patterns and predict subsequent events, storing and recalling of sequences are required (Hawkins, George, & Niemasik, 2009; Janacsek & Nemeth, 2012). Most predictions are based on the **implicit learning** that occurs when information is acquired from an environment of complex stimuli, without conscious access either to what was learned or to the fact that learning occurred. Implicit sequence learning underlies not only motor, but also cognitive and social skills; it is therefore an important aspect of life from infancy to old age. Most models and empirical studies of sequence learning highlight **the role of the basal ganglia** system, especially the striatum (Doyon et al., 2009).

Despite the growing interest in implicit learning in the past decades, there has been relatively little research on life-long development of implicit learning and on offline processing of implicitly learned information (i.e., consolidation). Here, we present three studies examining 1) implicit sequence learning across life-span, 2) the relationship between frontal-lobe functions and implicit sequence learning, and 3) the consolidation of implicitly learned material in healthy young and elderly adults (Table 1).

	Main question of the study	Participants	Methods	Results
Exp. I*	Age-related changes of implicit sequence learning across life span	N=421, from 4 to 85 years of age, clustered into 9 age groups	20 blocks of the ASRT task to measure implicit sequence learning	A gradual decline of sequence learning was found, with the highest learning performance in the 4- to 12-year-old age groups.
Exp. II**	How the disruption of frontal lobe functions by hypnosis affects implicit sequence learning?	N=14, highly hypnotizable university students (mean age=22 yrs, mean education=15 yrs)	15 blocks of the ASRT task to measure implicit sequence learning, separately in hypnotic and waking alert state (within-subject design)	Hypnosis boosted implicit sequence learning. This boosting effect was mediated by frontal lobe related executive functions.
Exp. III***	The time course of implicit sequence consolidation in healthy young and elderly adults	N=129, 71 young and 58 elderly adults; clustered into three conditions	25 blocks (Session 1) and 5 blocks (Session 2) of the ASRT task; between the two sessions there was a delay of either 12-, 24-hour or 1-week	Sequence-specific knowledge stabilized in young adults, but decreased in elderly, regardless of delay. General skill consolidation was time-dependent, with higher offline improvement after shorter delay in both age groups.

Table 1. The outline of the three experiments. *Janacsek, K., Fiser J., & Nemeth, D. (in press). *Developmental Science.* **Nemeth, D., Janacsek, K., Polner, B., & Kovacs, Z. A. (in press). *Cerebral Cortex.* ***Nemeth, D., & Janacsek, K. (2011). *Journal of Gerontology Series B: Psychological Sciences, 66B*(1), 15-22.

Experiment I

Two main approaches to implicit learning emerged in developmental neuroscience with a different assessment of **how learning abilities change with age**: 1) the developmental invariance model and 2) the age-related changes model. Studies supporting the developmental invariance model of implicit learning failed to find significant age-related differences in learning (Meulemans, Van der Linden, & Perruchet, 1998; Vinter & Perruchet, 2000). By contrast, the age-related changes models posit that considerable developmental differences can be observed in implicit learning with highest learning performance in adults (Fletcher, Maybery, & Bennett, 2000; Thomas et al., 2004). However, no previous studies have examined age-related differences from childhood to old age with identical methods. Therefore, in this study, we compared the implicit sequence learning from 4 to 85 years of age to determine age-related differences across human life span.

Methods

There were 421 participants from 4 to 85 years of age, clustered into 9 age groups (Table 1). We used the ASRT task (Howard & Howard, 1997; Nemeth et al., 2010) to measure implicit sequence learning. In this task a stimulus appeared in one of the four empty circles arranged in a line on a computer screen. The participants were instructed to respond to different stimulus events by pressing the corresponding response keys as fast and accurately as possible. The ASRT task consisted of 20 blocks. An eight-element alternating sequence repeated ten times within each block (e.g., 2R1R3R4R, where numbers represent stimulus locations, and R represent random).

Because of the alternating structure of the ASRT, some runs of events (called triplets) occur more often (high frequency triplets) than others (low frequency triplets). In this task, we can separate general skill learning from sequence-specific learning, where **general skill learning** refers to increasing speed as the result of practice, irrespectively of triplet-type. In contrast, **sequence-specific learning** refers to the acquisition of sequence-specific knowledge, resulting in relatively faster responses for more predictable high-frequency events compared to less predictable low-frequency events.

Results and Discussion

We found that the 4- to 12-year-old age groups showed the strongest sequence learning effect measured by the raw reaction times. Around the age of 12, we found a striking transition to less pronounced sequence-specific learning, which was further reduced in the oldest age group. Thus, in contrast to the developmental invariance and the age-related changes approaches, our results demonstrate a gradual decline in learning across the lifespan.

Sequence learning scores based on the accuracy and raw reaction time showed different curves: the former one is a bell-shaped curve, whereas the latter is a gradually declining curve. This difference can be explained by that more effective response selection processes are essential to achieve a higher general accuracy and also sequence-specific learning measured by accuracy. As response selection is mediated by frontal areas (e.g., anterior cingulate cortex, Aarts & Roelofs, 2011), the relatively weaker performance in children and elderly groups may be due to the underdeveloped/deteriorating attentional brain circuits connected to the frontal lobe. It is also in line with this assumption, that elderly groups could maintain a high general accuracy rate only with a trade-off in reaction time.

We propose that the raw RT difference between the high and low frequency triplets in the ASRT task is a measure of human sensitivity to the relative raw probabilities of events observed implicitly in their environment. Thus, our results show a marked decrease in this sensitivity around the age of 12, which might be explained based on a shift in the structural development of implicit learning. Recent studies proposed that using an internally stored structured model of the world (model-based learning) together with probabilistic model-free learning could help to address this issue and also provide evidence that humans might implement such a strategy shift during implicit learning (Orban, Fiser, Aslin, & Lengyel, 2008; Tenenbaum, Kemp, Griffiths, & Goodman, 2011). Importantly, it is known that the frontal cortical areas related to model-based learning become truly functional late in the development, around age of 12 (Blakemore & Choudhury, 2006), which is about the age when we found the sudden decrement in sequence-specific learning. We propose, that this enhanced functionality signals the shift when the system adapts efficiently to more complex aspects of the world by relying more on internal model-based interpretations, while somewhat neglecting the raw probabilities of the sensory input, and therefore, decreasing the ability to develop and stabilize fundamentally new basic competences. Thus the seemingly paradoxical result of gradually becoming less sensitive to basic statistics, if timed appropriately, could be the optimal strategy for human implicit learning in general (Figure 1).

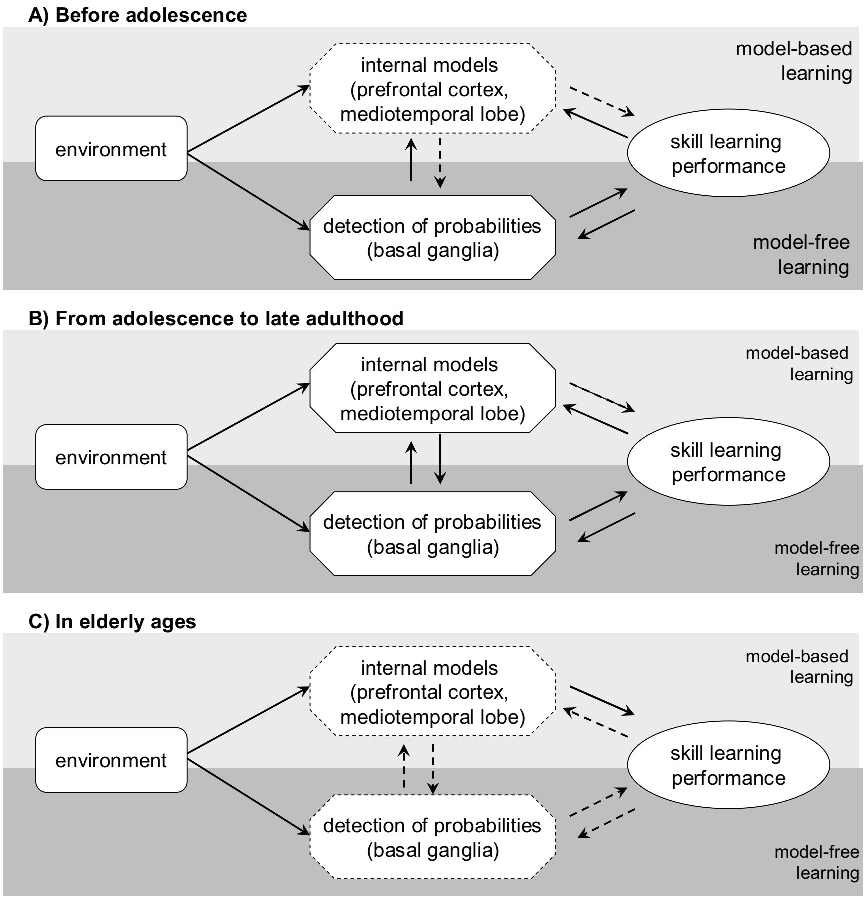

Figure 1. Competition between model-based and model-free neurocognitive subsystems of skill learning. (A) Before adolescence, underdeveloped internal models (dashed boundary) have little influence on interpretations of detected statistical probabilities of events in the environment (dashed arrows). Skill learning performance is determined by detection of probabilities. (B) From adolescence, well-developed internal models (solid boundary) strongly modulate the interpretations of observed statistics. This helps extracting complex relations but relatively impairs measuring and utilizing raw probabilities in skill learning (dotted arrow). (C) In older ages, skill learning performance decreases. This decline could be caused by the reduced sensitivity to statistical probabilities, increasingly rigid internal models and/or weaker connection between these systems.

What are the underlying mechanisms of the decreased performance of the elderly group? Several studies have found both structural and functional impairments in the fronto-striatal circuitry in older ages and there was also evidence for recruiting MTL to learn sequences implicitly (Dennis & Cabeza, 2011; Rieckmann, Fischer, & Bäckman, 2010). Within the proposed framework, these findings can be interpreted as a deterioration in three mechanisms that contribute to the age-related decline in skill learning: 1) reduced detection of probabilities, 2) rigidity of internal models and/or 3) more restricted connections between internal models and probability detection (Figure 1c).

Experiment II

As rapid and reversible changes of cognitive processing are encountered in hypnosis, this phenomenon is an excellent tool of research in the cognitive neurosciences. Regarding the neural background of hypnosis, studies demonstrated that people (especially with high susceptibility to hypnosis) show decreased performance on some frontal lobe-related tasks in hypnosis (Kaiser, Barker, Haenschel, Baldeweg, & Gruzelier, 1997). More recent studies suggest reduced functional brain connectivity between cortical areas in hypnosis, and this is especially typical for frontal areas. Hypnosis temporarily disconnects certain frontal areas from the anterior cingular cortex and other brain areas, disturbing the frontal attentional control and executive system (Egner, Jamieson, & Gruzelier, 2005; Kaiser et al., 1997).

Since a growing body of data has shown that frontal lobe-mediated processes are disrupted in hypnosis, we used hypnosis as a tool to reduce the competition between frontal lobe-related model-based and striatum-related model-free systems by comparing implicit sequence learning in hypnosis and in waking alert state.

Methods

Fourteen highly hypnotizable young adults performed the ASRT task both in waking alert and hypnotic state (Table 1). Similarly to previous studies we defined high hypnotizability as having 8 or higher score on the Harvard Group Scale of Hypnotic Susceptibility: Form A (HGSHS:A, Shor, Orne, & Press, 1962). In addition, executive functions were assessed by the Wisconsin Card Sorting Test (Heaton, Chelune, Talley, Kay, & Curtiss, 1993) and Verbal Fluency Task (Spreen & Strauss, 1991) in order to investigate the possible interactions between frontal lobe functions and the effect of hypnosis on sequence learning.

A skilled hypnotist therapist, who has extensive experience with hypnosis, tape-recorded the induction, instructions, and dehypnotizing phases. This recording was played to each participant. The type of hypnosis induction was essentially relaxational.

Results and Discussion

We found significant sequence-specific learning, which increased with practice. The learning in hypnotic and alert states differed significantly: sequence learning was 2.5-times higher under hypnosis than in the waking alert state. Participants with higher executive functions showed smaller sequence learning in the waking alert state compared to the hypnotic condition, while participants with lower executive functions showed similar extent of sequence learning.

Taken together, we found that hypnosis boosted sequence learning providing support for the idea that learning and memory processes may not only involve the engagement of specific neuroplastic mechanisms, but may also rely upon the disengagement of interacting systems (Brown & Robertson, 2007, p. 149). Our finding is in line with previous studies demonstrating that manipulations reducing the reliance on frontal lobe-dependent processes improved BG-dependent learning performance (e.g., Filoteo, Lauritzen, & Maddox, 2010). This interpretation is consistent with the result that participants with better frontal lobe related executive functions showed decreased sequence learning in the waking alert condition compared to the participants with lower executive functions. By contrast, in the hypnotic state, participants with higher executive functions shifted from relying on frontal lobe-related attentional processes to automatic, procedural-based mechanisms, resulting in enhanced sequence learning.

Experiment III

It is important to highlight that sequence learning does not occur only during practice, in the online periods, but also between practice periods, during the offline periods. The process that occurs during the offline periods is referred to as **consolidation**, which denotes the stabilization of a memory trace after the initial acquisition (Krakauer & Shadmehr, 2006; Nemeth et al., 2010). Studies on the time course of consolidation indicate that there is a "critical period" after the learning phase, which is necessary for the stabilization of memory traces. This time period depends on the task demand, and it varies from 1-2 hours to 5 hours or 6 hours (Robertson, Press, & Pascual-Leone, 2005; Shadmehr & Brashers-Krug, 1997). These results suggest that consolidation of sequence knowledge may be a dynamic process. However, these studies examined only a shorter stretch of time, so the question can be raised, what happens in consolidation after more than 12 hours. In addition, age-related differences in implicit sequence consolidation have not yet been comprehensively characterized.

In Experiment III we investigated consolidation of implicit sequence knowledge by comparing the performance after 12-, 24-hour, and 1-week delays from the initial learning session in young and elderly adults in order to determine age-related differences not only in online learning, but also in offline processing of the learned material. This research went beyond previous ones in that: 1) it used the ASRT task, which allowed to investigate sequence-specific and general skill learning separately, and 2) it compared three consolidation intervals to explore the time-dependent offline changes in more detail.

Methods

Seventy-one young and 58 elderly right-handed adults participated in the experiment (Table 1). There were two sessions in the experiment to examine the offline changes of implicit sequence learning: a learning phase (Session 1) and a testing phase (Session 2) separated by a 12-, 24-hour or 1-week interval offline period.

Results and Discussion

In the young adults, we found offline improvement of the general skill after all delays, with gradual decline among them. The elderly adults showed offline improvement of the general skill only after the 12-hour offline period, and this improvement was weaker than that in the young group. The differences among the 12-, 24-hour and 1-week offline intervals suggest that the consolidation of general skill learning is time-dependent. In addition, older participants are more sensitive for this offline time course in that they showed no offline improvement even after 24-hour delay. These results are congruent with recent theories of motor skill consolidation (Robertson et al., 2005; Shadmehr & Brashers-Krug, 1997) that claim that memory stabilization occurs during the first 5-6 hours after learning. The observed strong offline improvement after 12 hours may reflect this first stabilization process of memory traces, including the previously mentioned critical time period.

No offline improvement was found in sequence-specific learning in either age group with any of the consolidation intervals. Sequence-specific learning did not decrease significantly between sessions for young participants, suggesting that sequence-specific knowledge was well consolidated in this group, whereas the older group showed weaker consolidation in all delay conditions compared to the younger group. These results suggest that stabilization of sequence-specific memory is a faster process, whereas offline changes of general skill are more influenced by a longer stretch of time.

Interpreting our results in the framework proposed in Experiment I, there are at least three mechanisms which may underlie the age-related decline in the consolidation of skill learning on the functional level (cf. Figure 1c). As the initial level of learning performance was matched between young and elderly adults, the decrease in sequence knowledge after the consolidation period might be attributed to the rigidity of internal models or to the weaker connections than to the reduced probability detection itself. Thus, based on these consolidation results, we suggest that not only the model-free, but also the model-based learning is limited in older ages.

Conclusions

The following conclusions can be drawn based on the studies presented in this thesis:

1. We found dissociation between accuracy and RT learning measures in Experiment I.
2. Accuracy learning measures showed a typical bell-shaped curve across life span. This measure of implicit sequence learning may be connected to attentional resources to a higher extent.
3. Based on raw RT results we suggest that acquiring fundamentally new skills implicitly (i.e., relying less on attentional resources) is most effective before adolescence. The reduced learning after adolescence indicates a shift to relying more on internal model-based interpretations (connected to PFC/MTL structures), while somewhat neglecting the raw probabilities of the sensory input (mediated primarily by the BG).
4. In Experiment II we have shown that hypnosis boosted sequence learning in young adults, providing support for the idea that manipulations which reduce the reliance on frontal lobe-dependent processes improve BG-dependent learning performance.
5. Executive functions moderated the boosting effect of hypnosis; it was more pronounced in participants with higher executive functions.
6. Regarding the consolidation of implicit knowledge, offline improvement of the general skill was found after 12-, 24-hour and 1-week delay in young adults, with a gradual decline among them. The elderly adults showed offline improvement of the general skill only after the 12-hour offline period.
7. No offline improvement was found in sequence-specific learning in either age group with any of the consolidation intervals. Sequence-specific learning did not decrease significantly between sessions for young participants, whereas the older group showed weaker consolidation in all delay conditions compared to the younger group.
8. To sum up, our findings in Experiment III draw attention to the fact that the consolidation is not a single process; instead there are multiple mechanisms in offline learning (general skill, sequence-specific processes), which are differently influenced by aging and the course of time.

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Papers the thesis is based on:

I. **Janacsek, K.***, & Nemeth, D. (2012). Predicting the future: from implicit learning to consolidation. *International Journal of Psychophysiology, 83*(2), 213-221. DOI: 10.1016/j.ijpsycho.2011.11.012. Impact factor: 2.378.

II. **Janacsek, K.***, Fiser J., & Nemeth, D. (in press). The best time to acquire new skills: Age-related differences in implicit sequence learning across life span. *Developmental Science.* DOI: 10.1111/j.1467-7687.2012.01150.x. Impact factor: 3.53.

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IV. Nemeth, D., & **Janacsek, K.*** (2011). The dynamics of implicit skill consolidation in young and elderly adults. *Journal of Gerontology Series B: Psychological Sciences, 66B*(1), 15-22. DOI: 10.1093/geronb/gbq063. Impact factor: 1.963.

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Cumulative impact factor of Karolina Janacsek's all papers: 38.25

Papers related to the thesis:

I. Hallgató, E., Győri-Dani, D., Pekár, J., **Janacsek, K.***, & Nemeth, D. (in press). Perceptual – Motor learning debate in skill acquisition: the role of consolidation. *Cortex.* DOI: 10.1016/j.cortex.2012.01.002. Impact factor: 7.251.

II. Nemeth, D., **Janacsek, K.***, Csifcsak, G., Szvoboda, G., Howard, J. H. Jr., & Howard, D. V. (2011). Interference between sentence processing and probabilistic implicit sequence learning. *PLoS ONE, 6*(3): e17577. DOI: 10.1371/journal.pone.0017577. Impact factor: 4.411.

III. Nemeth, D., **Janacsek, K.***, Balogh, V., Londe, Zs., Mingesz, R., Fazekas, M., Jambori, Sz., Dányi, I., & Vetró, Á. (2010). Learning in Autism: implicitly superb. *PLoS ONE, 5*(7), e11731. Impact factor: 4.411.

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* - first author or equivalent (equal contribution)

Abstracts related to the thesis:

I. **Janacsek, K.**, & Nemeth, D. (2011). Well-established skills are resistant to disruption – evidence from a dual-task paradigm. *ICOM-5, International Conference on Memory*, 31 July – 06 August, York, UK.

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