Center for Lifespan Psychology

Director: *Ulman Lindenberger*

Research Scientists

Yana Fandakova
Elisabeth Wenger

Maike M. Kleemeyer
(as of 09/2019)
Corinna Laube
(01/2019–04/2020)
Ulman Lindenberger
Ziyong Lin
(as of 11/2018)

Neda Khosravani
Eleftheria Papadaki
(as of 11/2018)

Key Reference

Wenger, E., & **Kühn, S.** (in press). Neuroplasticity. In T. Strobach & J. Karbach (Eds.), *Cognitive training: An overview of features and applications* (2nd ed.). Springer.

Research Project 4: Mechanisms and Sequential Progression of Plasticity

This project addresses the questions of whether and how plasticity contributes to development across the lifespan. We use training studies as a method of choice to probe antecedents, mechanisms, and consequences of plastic change across different age groups and functional domains. Special attention is given to the dynamics of plastic changes across structural, functional, and behavioral levels of analysis.

The human brain is plastic—it possesses the capacity to implement lasting structural changes in response to environmental demands that alter its functional and behavioral repertoire (Lindenberger & Lövdén, 2019; Wenger & Kühn, in press). We assume that plasticity is induced by a mismatch between environmental demands and an individual's current behavioral and neural resources. It is metabolically costly and competes with the need for stability, which facilitates the development of a well-orchestrated set of habits and skills. The resulting interplay of mechanisms promoting plasticity versus stability organizes development into multiple alternating and sequentially structured periods that together support the hierarchical organization of cerebral functions and behavior (Lindenberger, 2018).

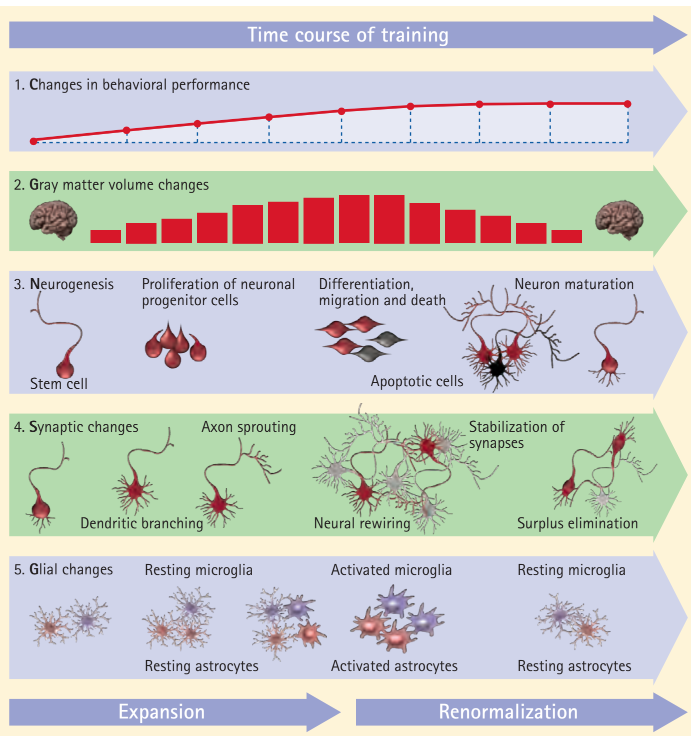

Figure12. Schematic illustration of potential cellular changes underlying gray matter volume expansion and renormalization as detectable with magnetic resonance (MR) images (adapted from Wenger, Brozzoli et al., 2017).

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Plasticity in the Motor Domain

The acquisition of skilled motor performance provides a rich testing ground for exploring the mechanisms and progression of plasticity. In a pioneering study, we acquired up to 18 structural magnetic resonance (MR) images over a 7-week period while 15 right-handed participants practiced left-hand writing and drawing (Wenger, Kühn et al., 2017). After 4 weeks of training, we observed increases in gray matter in both the left and right primary motor cortices relative to a control group; another 3 weeks later, these differences were no longer reliable. Time-series analyses confirmed that gray matter in both primary motor cortices expanded during the first 4 weeks and then partially renormalized, in particular in the right hemisphere, in the presence of continued practice and increasing task proficiency. Based on this pattern, which is in good agreement with macroscopic and microscopic curvilinear changes observed in nonhuman primates and rodents, we have proposed that plastic changes might often follow a sequence of initial tissue expansion, selection of the most suitable circuitry, and partial or complete renormalization to baseline levels (see Figure 12; Wenger, Brozzoli et al., 2017; see also Lindenberger & Lövdén, 2019).
Motor skill acquisition involves brain regions that vary considerably in their developmental trajectories during childhood. Frontal regions, which dominate initial learning and are thought to contribute to the demand–capacity mismatch representation that triggers a plastic response, mature relatively late in childhood (Fandakova et al., 2018).

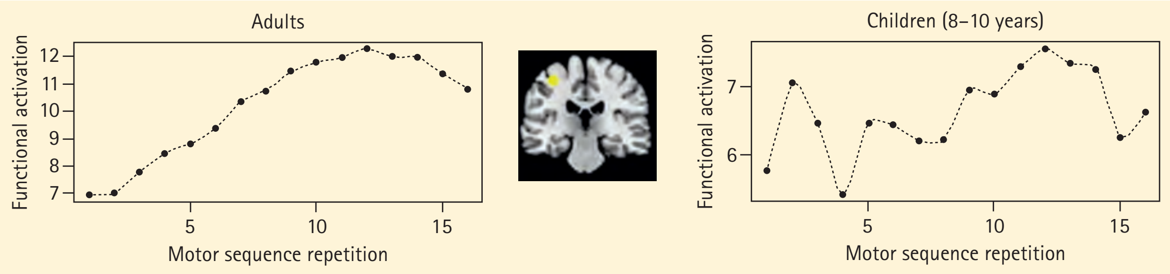

Figure 13. The learning of a novel motor sequence is associated with greater changes in left motor cortex activity in adults than in children. While adults' motor cortex activity increased with the repeated execution of the sequence and increasing proficiency, children's motor cortex was already engaged early on during learning.

In contrast, primary motor regions, which dominate later phases of learning, mature relatively early. To evaluate the consequences of these maturational differences, we have examined age differences in motor sequence learning between young adults and children (8–10 years). Preliminary results suggest that both children and adults show decreasing frontal activation with increasing task proficiency. However, while adults showed a corresponding selective increase in motor cortex activation over time, children activated primary motor cortex both during early and late phases of learning (see Figure 13). In the context of extended skill acquisition, these age differences in activation may suggest that structural plastic changes in primary motor areas manifest themselves/occur earlier in children than in young adults.

Plasticity in the Auditory Domain

Music expertise relies on several sensory systems and the motor system and also poses high demands on control processes. Therefore, it offers a promising model for studying how specific forms of experience interact with preexisting individual differences to mold the structure and function of the brain. In an initial investigation, we investigated plastic changes in aspiring professional musicians who were preparing intensely for a highly competitive entrance exam at a university of the arts in comparison to skilled amateur musicians. Over the course of 6 months, we observed decreases in gray matter in the aspiring professional musicians in the left planum polare, posterior insula, and left inferior frontal orbital gyrus. The left planum polare, where the largest cluster of structural change was found, also showed increasing functional connectivity to other regions known to contribute to music expertise (see Figure 14). This increased connectivity was also reflected in analyses based on graph theory, pointing to the participation of the planum polare in a complex network. These results may provide further evidence for the expansion–renormalization pattern of brain structure in humans in the auditory domain if we assume that we captured the second portion of an expansion–renormalization cycle.

In a study that is currently underway, we aim to delineate patterns of plasticity over time in both the auditory and the visual domain and to better characterize the interplay between structural and functional plastic changes (Dissertation Eleftheria Papadaki). A group of young adults will be trained to discriminate between short melodies based on so-called microtonal intervals, which are considerably smaller than one semitone. During the 8-week training period, participants will undergo weekly structural and functional MR assessments. A second group will be trained in a visual discrimination task and will also be scanned eight times during the training period, allowing us to probe the applicability of the expansion–renormalization model in yet another sensory domain.

Boosting Plasticity in the Aging Brain

In the context of "Energizing the Hippocampus in Aging Individuals (EnergI)," a consortium funded by the Federal Ministry of

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Fandakova, Y., Bunge, S. A., Wendelken, C., Desautels, P., Hunter, L., Lee, J. K., & Ghetti, S. (2018). The importance of knowing when you don't remember: Neural signaling of retrieval failure predicts memory improvement over time. *Cerebral Cortex, 28*(1), 90–102. https://doi.org/10.1093/cercor/bhw352

Wenger, E., Brozzoli, C., **Lindenberger, U.,** & **Lövdén, M.** (2017). Expansion and renormalization of human brain structure during skill acquisition. *Trends in Cognitive Sciences, 21*(12), 930–939. https://doi.org/10.1016/j.tics.2017.09.008

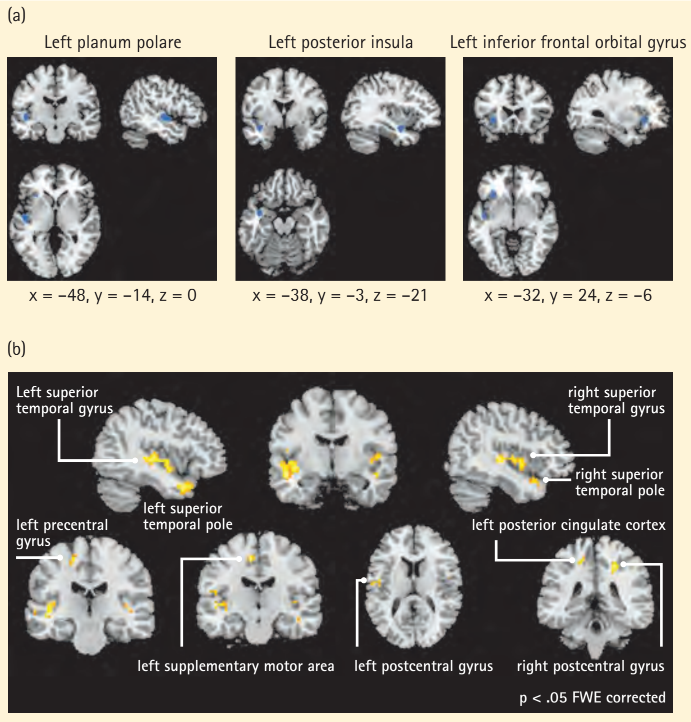

Figure 14. (a) While preparing for their entrance exam, aspiring professional musicians showed decreases in gray matter in the left planum polare, posterior insula, and left inferior frontal orbital gyrus. (b) In the aspiring professionals, but not among the amateur musicians, the biggest cluster of structural change, the left planum polare, showed increasing functional connectivity to the left and right auditory cortex, left precentral gyrus, left supplementary motor cortex, left and right postcentral gyrus, and left cingulate cortex.

Key Reference

Fandakova, Y., Selmeczy, D., Leckey, S., Grimm, K. J., Wendelken, C., Bunge, S. A., & Ghetti, S. (2017). Changes in ventromedial prefrontal and insular cortex support the development of metamemory from childhood into adolescence. *Proceedings of the National Academy of Sciences (USA), 114*(29), 7582–7587. https://doi.org/10.1073/pnas.1703079114

Education and Research, we also conducted a large-scale training study with 160 healthy older adults. Inspired by rodent models of environmental enrichment, the central goal of this study is to test the hypothesis that plastic changes in the hippocampal formation are more easily induced when an aerobic fitness intervention is combined with a cognitive intervention. Participants were randomly assigned to one of four groups: a combined language-learning and bicycle ergometer training group; a bicycle-ergometer only group; a language-learning only group; and an active control group participating in a book club. The study was carried out in 2017 and 2018 and allowed participants to make the training programs an integral part of their daily lives using tablets with a language-learning app and bicycle ergometers deployed at their homes. The data set comprises:
(a) structural MR measurements taken before training (pretest), after 3 months of training, and after 6 months of training (posttest);
(b) multiple cognitive and physical fitness measures assessed before and after training; and (c) day-to-day data on training intensity, training duration, and motivational states.
Data analyses are currently underway, with special attention given to the joint effects of the two interventions and the specific effects of physical exercise (Dissertation Sarah Polk, supervised by Sandra Düzel, BASE-II project).

Plasticity in Task-Switching in Childhood
Childhood is characterized by maturational changes in brain structure and function and in the organization of behavior. These developmental changes are particularly pronounced for cognitive control processes, such as the ability to flexibly shift between different task sets, and their neural manifestations (Fandakova et al., 2017). In collaboration with Silvia Bunge, University of California, Berkeley, USA, we have conducted a training study to examine individual differences in behavioral and neural manifestations of task-switching plasticity in 200 children aged 8 to 11 years (Dissertation Neda Khosravani). In a total of 27 sessions spread out over 9 weeks, children in the experimental group practiced switching among sets of different tasks. The performance of children in this group will be compared to children in the active control group, who trained the identical tasks but without the need to constantly switch among them, and children in a passive control group, who did not practice any of the tasks. To assess training progress, all children were assessed behaviorally four times during practice. In addition, about half of the participants in each group also underwent functional and structural MR measurements four times.
One of the goals of this study is to extend the observation of the temporal progression of behavioral and neural manifestations of plasticity into childhood.
In collaboration with the *Brain Imaging Methods* project (see pp. 149 ff.) we also adopted a novel imaging sequence for this study to examine practice-related changes in

the myelination of cortical gray matter over time. Based on recent findings that individual differences in the fidelity with which incoming visual information is represented in the brain contributes to learning success in childhood (Fandakova et al., 2019), we aim to relate practice-related structural changes to changes in task-set representations over time. With respect to behavioral manifestations of plasticity, ongoing analyses focus on individual differences in the trajectory of practice-related change across practice sessions and how they are related to untrained measures of task-switching, processing speed, and cognitive control.

Furthermore, we also seek to understand how task-switching plasticity is modulated by gonadal hormone changes associated with puberty onset. Puberty onset typically occurs at around 8 years of age, with considerable variation in onset age across individuals. We collected saliva and hair samples to measure pubertal status via gonadal hormones and to examine whether individual differences in pubertal status are associated with behavioral and neural markers of plasticity. Here, we are particularly interested in testing the hypothesis that gonadal hormone changes associated with puberty onset influence cognitive development by altering the potential for plastic change (Laube, van den Bos, & Fandakova, 2020).

Curiosity and Surprise in Childhood

Along with surprise, curiosity, or the desire to acquire new information, may play an important role for learning and plasticity, especially during the early phases of a plastic episode when individuals are exploring the task space. We used trivia questions to examine the effects of curiosity and surprise on learning in children aged 10 to 14 years. Children of all ages showed better memory for questions that they were curious about. In contrast, higher post-answer surprise, or the discrepancy between children's initial curiosity and the interest in the actual trivia answer, benefited learning more strongly in adolescents than in children (see Figure 15). Following up on these findings, we are currently investigating how curiosity and surprise can be harnessed to facilitate learning and generalization of scientific concepts in adolescence.

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Fandakova, Y., Leckey, S., **Driver, C. C.,** Bunge, S. A., & Ghetti, S. (2019). Neural specificity of scene representations is related to memory performance in childhood. *NeuroImage, 199,* 105–113. https://doi.org/10.1016/j.neuroimage.2019.05.050

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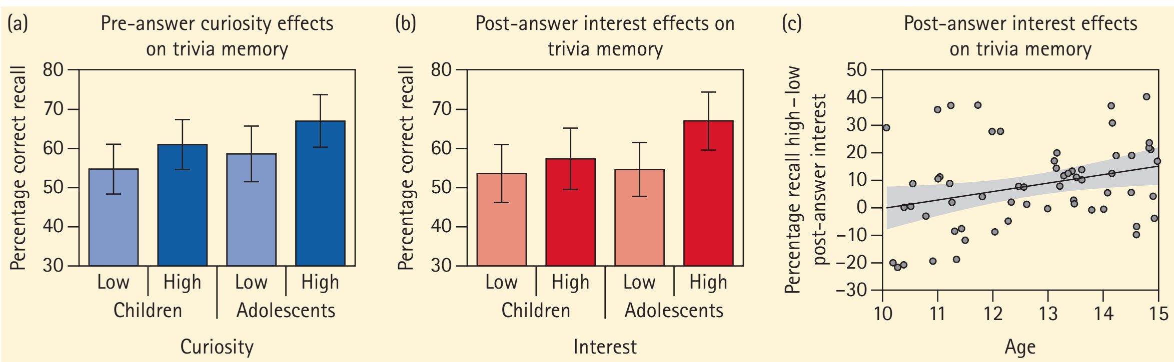

Figure 15. Children showed greater learning benefits for trivia questions that they were more curious about. In adolescents, learning was also modulated by how interesting they thought the actually presented answer was, such that they were more likely to remember the answer when initial curiosity was low but post-answer interest was high. In contrast, learning in younger children depended primarily on their initial curiosity and less so on post-answer interest.