Center for Lifespan Psychology

Director: *Ulman Lindenberger*

Research Team 2017–2019/20

Nils C. Bodammer, Andreas M. Brandmaier, Julia A. M. Delius, Charles C. Driver, Sandra Düzel, Yana Fandakova, Douglas D. Garrett, Imke Kruse (Head of Research Planning and Research Coordination), Simone Kühn (as of 02/2017: University Medical Center Hamburg-Eppendorf (UKE), Germany; since 01/2019: Lise Meitner Group for Environmental Neuroscience), **Ulman Lindenberger,** Viktor Müller, Naftali Raz, Myriam C. Sander, Katrin Schaar (as of 08/2019: Technische Universität Berlin, Germany, Julius Verrel (as of 04/2017: Universität zu Lübeck, Germany), Gert G. Wagner (Max Planck Fellow), Elisabeth Wenger, Markus Werkle-Bergner, André Werner

Postdoctoral Fellows
Janne Adolf (LIFE; as of 11/2017: KU Leuven, Belgium), Caroline Beese, Andrew R. Bender (as of 02/2018: Michigan State University, East Lansing, USA), Julia C. Binder (as of 03/2017: Merck [Schweiz] AG, Switzerland), Whitney G. Cole (as of 03/2018: New York University, USA), Martin J. Dahl, Marie K. Deserno, Julian D. Karch (as of 07/2017: Leiden University, Netherlands), Attila Keresztes (as of 12/2018: Hungarian Academy of Sciences, Budapest, Hungary), Maike M. Kleemeyer, Niels A. Kloosterman, Ylva Köhncke, Corinna Laube (as of 05/2020: Hochschule Fresenius, Hamburg, Germany), Ziyong Lin, Kristoffer N. T. Månsson, Beate E. Mühlroth (as of 04/2020: Bundespsychotherapeutenkammer, Berlin, Germany), Chi (Zoe) Ngo, Alistair Perry (as of 04/2020 University of Cambridge, UK), Laurel Raffington (as of 01/2019: The University of Texas at Austin, USA), Davide Santoro, Caroline Szymanski (as of 08/2018: Hasso Plattner Institute, Potsdam, Germany), Leonhard Waschke, Claudia Wehrspaun (until 03/2020), Iris Wiegand

Predoctoral Fellows
Rasmus Bruckner (guest, as of 05/2019: Freie Universität Berlin, Germany), Elisa S. Buchberger (LIFE), Oisin Butler (LIFE; as of 03/2019: Bayer AG, Berlin, Germany), Maike Hille (LIFE), Ann-Kathrin Jöchner (LIFE), Anna Karlsson (LIFE), Neda Khosravani (LIFE), Malte Kobelt (guest, as of 04/2020: Ruhr-Universität Bochum, Germany), Julian Q. Kosciessa (COMP2PSYCH), Lanfang Liu (guest, as of 01/2018: Beijing Normal University, China), Eleftheria Papadaki (LIFE), Claire Pauley (LIFE), Sarah Polk (LIFE), Liliana Polyanska (COMP2PSYCH), Alexander Skowron (LIFE/COMP2PSYCH), Verena R. Sommer (LIFE)

Associate Research Scientists
Annette Brose (Humboldt-Universität zu Berlin, Germany), Mara Mather (University of Southern California, Los Angeles, USA), Florian Schmiedek (German Institute for International Educational Research, Frankfurt a.M., Germany, affiliated until 12/2019), Sascha Schroeder (University of Göttingen, Germany), Yee Lee Shing (Goethe University Frankfurt am Main, Germany, affiliated until 12/2019), Julius Verrel (Universität zu Lübeck, affiliated until 12/2017), Manuel C. Völkle (Humboldt-Universität zu Berlin, Germany, affiliated until 12/2019), Timo von Oertzen (Universität der Bundeswehr München, Germany)

Visiting Researchers
Steven M. Boker (University of Virginia, Charlottesville, USA), Timothy R. Brick (The Pennsylvania State University, USA), Silvia Bunge (University of California, Berkeley, USA), Roberto Cabeza (Duke University, Durham, USA), Michael Frank (Stanford University, Stanford, USA), Adam Gazzaley (University of California, Oakland, USA), Christopher Hertzog (Georgia Institute of Technology, Atlanta, USA), Gerd Kempermann (Deutsches Zentrum für Neurodegenerative Erkrankungen, Dresden, Germany), Jutta Kray (Saarland University, Saarbrücken, Germany), Suresh Krishna (Cognitive Neuroscience Laboratory, Göttingen, Germany), Antonio Krüger (German Research Center for Artificial Intelligence, Saarbrücken, Germany), Ulrich Mayr (University of Oregon, Eugene, USA), Axel Mecklinger (Saarland University, Saarbrücken, Germany), Thad A. Polk (University of Michigan, Ann Arbor, USA), Tomás Ryan (Trinity College Dublin, Ireland), Jeffrey A. Stanley (Wayne State University, Detroit, USA), Tadashi Suzuki (Shirayuri University, Tokyo, Japan), Elliott Tucker-Drob (The University of Texas at Austin, USA), Fredrik Ullén (Karolinska Institutet, Stockholm, Sweden), Hubert D. Zimmer (Saarland University, Saarbrücken, Germany)

> "But … its eminent modifiability, and its predisposition to self-initiated action, may it develop little or much, and may it differ in amount between different individuals, is among the immutable features of humankind, which can be found wherever humans exist."
> *Johann Nicolaus Tetens, 1777, I, p. 766*

J. N. Tetens (1736–1807), philosopher of the Enlightenment Era

Introductory Overview

Founded in 1981 by Paul B. Baltes (1939–2006), the Center for Lifespan Psychology (LIP) pursues lifespan psychology as a distinct conceptual approach within developmental psychology. Since 2004, the Center has continuously extended its research program into developmental and cognitive neuroscience. The Center hosts the Max Planck UCL Centre for Computational Psychiatry and Ageing Research led by Raymond Dolan and Ulman Lindenberger, which was founded in 2014 and is located in both London and Berlin (see pp. 177 ff.). LIP also is involved in the longitudinal Cognition, Brain, and Aging (COBRA) study, which investigates the role of dopamine in cognitive aging. COBRA is conducted in Umeå, Sweden, and involves scientists from Umeå University, from the Aging Research Center at Karolinska Institutet, Stockholm, and from LIP. The Center continues to pay special attention to the age periods of late adulthood and old age, which offer unique opportunities for innovation, both in theory and practice. At the same time, it has continually strengthened its focus on the operation of maturational mechanisms during childhood, especially in relation to memory development.

Key Reference

Schmiedek, F., Lövdén, M., **von Oertzen, T.,** & **Lindenberger, U.** (in press). Within-person structures of daily cognitive performance differ from between-person structures of cognitive abilities. *PeerJ.*

Three Guiding Propositions

The Center's research agenda can be summarized by three interrelated theoretical propositions (Lindenberger et al., 2006). In line with general tenets of lifespan psychology, these propositions emphasize conceptual and methodological issues in the study of lifespan behavioral development and thereby provide a conceptual foundation for formulating research questions in specific domains of interest.

Proposition 1: Lifespan Changes in the Individual's Behavior as Interactions Among Maturation, Learning, and Senescence

The general goal of developmental psychology is to identify mechanisms that generate invariance and variability, constancy and change, in behavioral repertoires from infancy to old age. By identifying the commonalities, differences, and interrelations in the ontogeny of sensation, motor control, cognition, affect, and motivation, both within and across individuals, developmental psychologists and developmentally oriented neuroscientists attempt to arrive at more or less comprehensive theories of behavioral development. To provide explanations that qualify as psychological and developmental, the effects of agents external to the developing individual, such as educational policies (Lövdén et al., in press), parents' affect attunement, teachers' classroom behavior, or a state's retirement policies, need to be mapped onto mechanisms and organizational laws that operate and evolve within individuals. Hence, as John Nesselroade, Peter Molenaar, and others have emphasized, developing individuals are the privileged system for description, explanation, and intervention (Schmiedek et al., in press; Voelkle et al., 2018).
Individuals organize their exchange with the physical and social environment through behavior (see Figure 1). On the one hand, the changing brain and the changing physical and cultural environment shape behavioral development. On the other hand, behavior alters both the brain and the environment. Hence, environment and brain act as antecedents but also as consequents of moment-to-moment variability and long-term changes in patterns of behavior. The components of this system, brain, behavior, and environment, are constantly coupled and cannot be reduced onto each other, as they jointly condition an individual's life trajectory through recursive self-regulation.

Key Reference

Lindenberger, U., Li, S.-C., & Bäckman, L. (2006). Delineating brain–behavior mappings across the lifespan: Substantive and methodological advances in developmental neuroscience. *Neuroscience & Biobehavioral Reviews, 30*(6), 713–717. https://doi.org/10.1016/j.neubiorev.2006.06.006

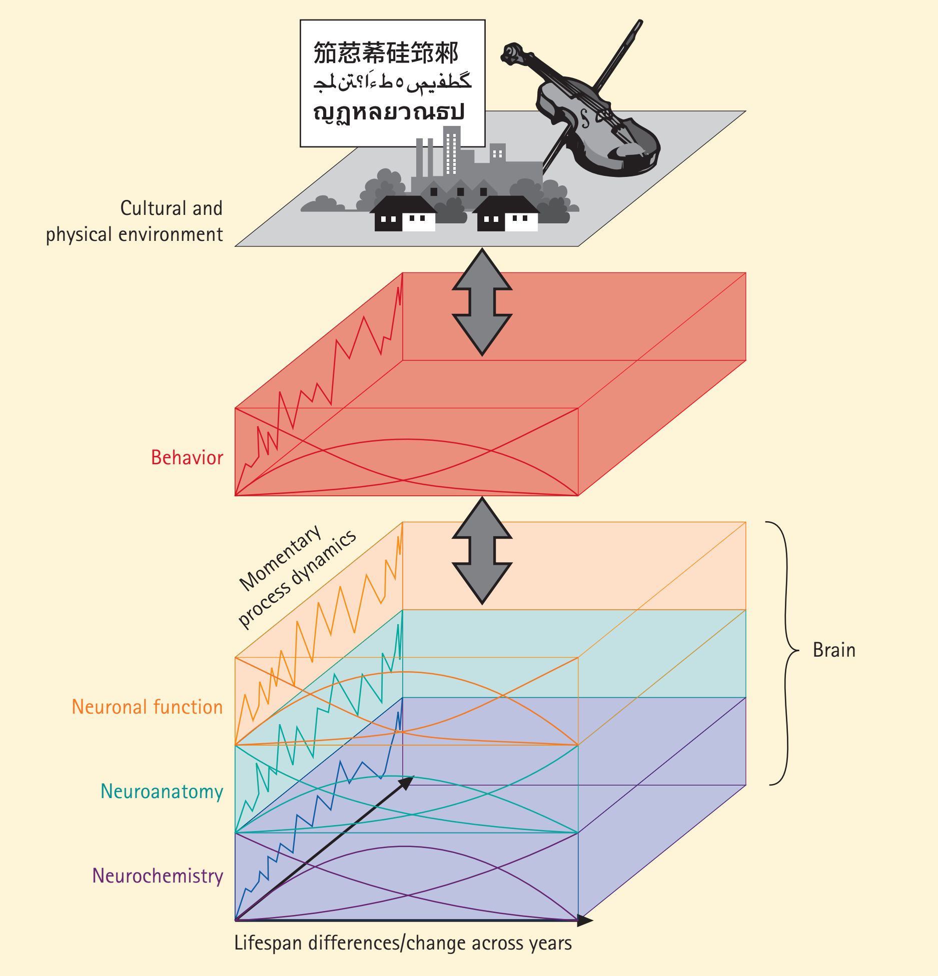

Figure 1. Environment and brain as antecedents and consequents of moment-to-moment variability and long-term changes in patterns of behavior. Lifespan changes in brain–behavior mappings are shaped by interactions among processes related to maturation, learning, and senescence. The identification of key players in the ontogeny of brain–behavior dynamics requires a coalition between formal tools for synthesis across levels of analysis and timescales as well as empirical methods to study variability and change in brain and behavior (adapted from Lindenberger et al., 2006).

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In attempts to explain the age-graded evolution of this system, *maturation* and *senescence* denote the operation of age-graded brain mechanisms and their effects on changes in behavior, which are especially pronounced early and late in life. In addition, *learning*, at any point during ontogeny, denotes changes in brain states induced by behavior–environment interactions. Maturation cannot take place without learning, and learning cannot take place without maturation. Similarly, the ways in which senescence takes its toll on the brains of aging individuals depends on their past and present learning and maturational histories. To complicate matters, processes commonly associated with maturation are not confined to early ontogeny, and processes related to senescence are not restricted to old and very old age. For instance, neurogenesis and synaptogenesis, which qualify as maturational mechanisms promoting plasticity, continue to exist in the adult and aging brain; conversely, declines in dopaminergic neuromodulation, which indicate senescence-related changes in brain chemistry, commence in early adulthood.

Thus, maturation, senescence, and learning mutually enrich and constrain each other throughout the entire lifespan and must be understood and studied as interacting forces constituting and driving the brain–behavior–environment system. Psychologists occupy a central position in this endeavor because they possess a rich and adequate repertoire of experimental and methodological tools to describe and modify the organization of behavior (Voelkle et al., 2018). In particular, direct comparisons between children and older adults help to identify commonalities and differences in the mechanisms that drive child and adult development.

Proposition 2: Lifespan Theory and Methodology Need to Integrate Evidence Across Domains of Functioning, Timescales, and Levels of Analysis

Developmental psychology is faced with three challenging integrative tasks. First, there is the need to integrate theorizing and research practice across functional domains to attain a comprehensive picture of individual development. For instance, sensorimotor and cognitive functioning are more interdependent in early childhood and old age than during middle portions of the lifespan, and developmental changes in either domain are better understood if studied in conjunction. Similar observations can be made for many other domains of functioning whose changes have generally been studied in isolation, such as the ontogeny of social interaction and cognition; of emotion regulation and motivational states; or of memory, working memory, and attention.

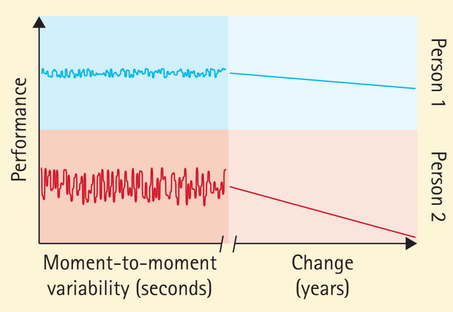

Figure 2. Example for predictions linking moment-to-moment variability to long-term change and brain changes to behavioral changes. Aging individuals with greater moment-to-moment fluctuations in behavior at a given point in time are expected to show greater subsequent longitudinal decline in mean levels of functioning than individuals who fluctuate less (adapted from Lindenberger et al., 2006).

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Second, there is a need to understand the mechanisms that link short-term variations to long-term change. Short-term variations are often reversible and transient, whereas long-term changes are often cumulative, progressive, and permanent. Establishing links between short-term variations and long-term changes is of eminent heuristic value, as it helps to identify mechanisms that drive development in different directions. For instance, aging cognitive systems show a decrease in processing robustness, which may signal impending long-term changes in other characteristics of the system (see Figure 2). To articulate these different timescales, we need to gather multivariate time-series data that capture short-term variability and long-term changes in cross-domain dependencies.

Third, to arrive at mechanistic explanations of behavioral change, there is the need to integrate behavioral and neural levels of analysis. At any given point in the lifespan, one-to-one mappings between brain states and behavioral states are the exception rather than the rule, as the brain generally explores and offers more than one implementation of an adaptive behavioral outcome (Lindenberger & Lövdén, 2019). Therefore, ontogenetic changes in behavioral repertoires are accompanied by continuous changes in multiple brain–behavior mappings. Some of these remapping gradients may be relatively universal and age-graded, whereas others may be more variable, reflecting genetic differences, person-specific learning histories, the path-dependent nature of developmental dynamics, or a combination of all three. The resulting picture underscores the diversity and malleability of the organization of brain and behavior as well as the constraints on diversity and malleability brought about by (a) universal age-graded mechanisms associated with maturation and senescence, (b) general laws of neural and behavioral organization, and (c) sociocultural as well as physical regularities of the environment.

Key Reference

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Lindenberger, U., & **Lövdén, M.** (2019). Brain plasticity in human lifespan development: The exploration–selection–refinement model. *Annual Review of Developmental Psychology, 1,* 197–222. https://doi.org/10.1146/annurev-devpsych-121318-085229

Proposition 3: The Exploration of Age-Graded Differences in Plasticity Is a Powerful Tool for Identifying Mechanisms of Development

Both from scientific and societal perspectives, plasticity, or the alteration of developmental trajectories through experience, is a precious phenomenon (Lindenberger, 2014). Scientifically, inquiries into the plasticity of brain and behavior are rich sources of developmental information. Through the assessment of "changes in change," they offer the promise to observe the operation and proximal consequences of developmental mechanisms. For instance, studies in which research participants of different ages are instructed and trained to perform one or more cognitive tasks come with important validity benefits, such as (a) an increase in experimental control, (b) the identification of age differences near asymptotic performance levels, and (c) the assessment of transfer and maintenance effects. If neurochemical, neuroanatomical, and neurofunctional imaging measures are assessed before, during, and after training, intervention studies also offer new insights into relations between behavioral and neural manifestations of plasticity. By partly taking control over behavior–environment interactions, mechanisms of learning can be studied in the context of maturation and senescence (Lindenberger, 2018).

From the larger perspective of societal evolution, cognitive intervention studies explore the range of possible development, or what could be possible in principle if conditions were different (see Figure 3). Hence, investigations of age changes in the plasticity of development carry the potential to explain and ameliorate the expression of human potential.

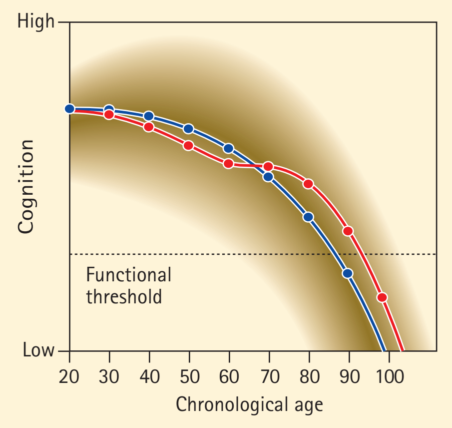

Figure 3. An individual's range of possible cognitive developmental trajectories from early to late adulthood. The blue curve shows the most likely developmental path under normal circumstances. The fading of the background color indicates that more extreme paths are less likely. The functional threshold represents a level of functioning below which goal-directed action in the individual's ecology will be severely compromised. The red curve represents the hope that changes in organism–environment interactions during adulthood move the individual onto a more positive trajectory. Beneficial changes may consist in the mitigation of risk factors, such as vascular conditions, metabolic syndrome, or chronic stress; the strengthening of enhancing factors, such as neuroplasticity; or both (adapted from Lindenberger, 2014).

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Conceptual Innovation

During the reporting period, the Center has sought to continue to contribute to conceptual innovation and integration in lifespan psychology and developmental neuroscience. In the following, we highlight three examples.

The exploration–selection–refinement model of human brain plasticity. In recent years, the project on plasticity in LIP (pp. 142 ff.), in collaboration with the laboratory led by Martin Lövdén in Sweden (see https://lovdenlab.org), has launched a new generation of experimental studies that combine behavioral skill training with repeated functional and structural imaging to directly observe the temporal progression of plasticity in humans; for a pioneering study, see Wenger, Kühn et al. (2017). To guide this work, Ulman Lindenberger and Martin Lövdén have proposed the exploration–selection–refinement model (ESR) of plastic change (Lindenberger & Lövdén, 2019). Lindenberger and Lövdén note that plasticity cannot be conceived as a process of perpetual growth, given the large number of skills humans acquire during their lifetime (see also Wenger, Brozzoli et al., 2017). Instead, the ESR model posits that local plastic change proceeds in three phases that together form a learning cycle (see Figure 4). Early in learning, available neuronal microcircuits potentially capable of implementing the computations needed to execute

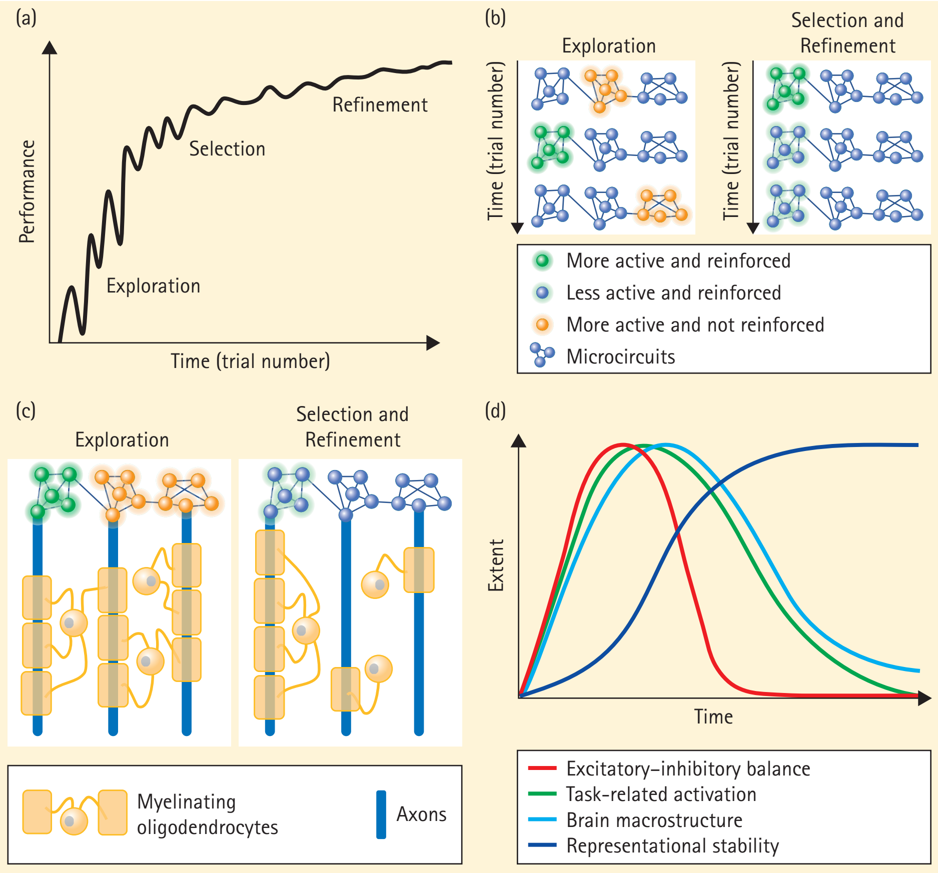

Figure 4. The exploration, selection, and refinement (ESR) model of human brain plasticity. According to the model, local plastic change proceeds in three phases that together form a learning cycle. During the initial stages of the exploration phase, when the brain activates available microcircuits, there is substantial trial-to-trial variability in (a) behavior and in (b) patterns of neural activity. Facilitated by shifts in excitatory-inhibitory balance, this heightened level of activity induces structural change, such as the formation of new dendritic spines as well as other structural characteristics of the neuron, exemplified by myelination in panel c. Through a process of reinforcement learning that is partly mediated by the neurotransmitter dopamine, the best performing microcircuit is selected, and neural and behavioral variability starts to decrease (panels a and b). In a subsequent refinement stage, processing in the selected microcircuit stabilizes while novel structures of unselected microcircuits continue to retract (panel c). (d) At the macroscale of magnetic resonance imaging, the ESR model predicts curvilinear changes in functional activation, brain metabolites, and volume, in conjunction with a late-evolving monotonic increase in similarity of neural activation patterns (reproduced with permission from Lindenberger & Lövdén, 2019).

a task are widely probed, and new circuits are formed, leading to an increase in gray-matter volume. During this exploration phase, there is substantial trial-to-trial variability in patterns of neural activity in these regions as well as in behavior. Exploration is deemed critical for acquiring new skills and might serve as a physiological substrate of exploration in the decision-theoretical sense, as skill acquisition generally requires the acquisition of complex rules, which only pays off in the long term. Exploration is followed by phases of experience-dependent selection and refinement of reinforced microcircuits and the gradual elimination of novel structures associated with unselected circuits, which may manifest as a decrease in gray-matter volume. The assumptions and hypotheses of the ESR will be computationally modeled and empirically tested in coming years.

Successful cognitive aging: The importance of maintenance. Together with Lars Nyberg from

Umeå University and others, researchers in LIP have emphasized brain maintenance as a key mechanism of successful cognitive aging. The notion of brain maintenance rests on the observation that individuals who show a relative lack of senescent brain changes also show more youth-like brain activation patterns and higher levels of cognitive performance. Brain maintenance is assumed to operate both at the general level of brain metabolism (Raz & Daugherty, 2018) and at the level of specific circuits and functions, such as the hippocampal formation, where it helps to preserve episodic memory (Nyberg & Lindenberger, 2020). Physical exercise is likely to foster brain maintenance by reducing vascular risks (Köhncke et al., 2018). Maintenance might operate in concert with other meta-mechanisms of successful cognitive aging, such as compensation and reserve. Attempts to discriminate among these mechanisms and compare their heuristic and explanatory value are underway (Cabeza et al., 2018).

Revisiting the dedifferentiation hypothesis of cognitive aging. About two decades ago, Shu-Chen Li and colleagues introduced a connectionist model of cognitive aging based on the observation that dopaminergic neuromodulation decreases throughout adulthood and old age (Li et al., 2001). Based on this model, it is hypothesized that declines in neuromodulation lead to dedifferentiated neural representations and processing pathways, thereby strengthening the variance that is shared across tasks. Using electroencephalography and functional magnetic resonance imaging, ongoing work by Minerva group leader Myriam Sander and colleagues within the LIME project investigates the core proposition of this line of reasoning, which states that individual neural representations become less distinct from one another with advancing adult age. A recent meta-analysis of correlated cognitive change in adulthood and old age, carried out by Elliot Tucker-Drob, Andreas Brandmaier, and Ulman Lindenberger (2019), is also relevant in this context. The authors found that an average of 60% of the between-person variation in change is shared across cognitive abilities (for details, see pp. 153 f.). In line with the dedifferentiation hypothesis, the proportion of shared variance in cognitive change increased from approximately 45% at age 35 years to approximately 70% at age 85 years.

Key References

Li, S.-C., Lindenberger, U., & Sikström, S. (2001). Aging cognition: From neuromodulation to representation. *Trends in Cognitive Sciences, 5*(11), 479–486. https://doi.org/10.1016/S1364-6613(00)01769-1

Nyberg, L., & **Lindenberger, U.** (2020). Brain maintenance and cognition in old age. In D. Poeppel, G. Mangun, & M. Gazzaniga (Eds.), *The cognitive neurosciences* (6th ed., 81–89). MIT Press.

Tucker-Drob, E. M., **Brandmaier, A. M.,** & **Lindenberger, U.** (2019). Coupled cognitive changes in adulthood: A meta-analysis. *Psychological Bulletin, 145*(3), 273–301. https://doi.org/10.1037/bul0000179

Research Awards (Selection)

In 2017, Markus Werkle-Bergner received a Research Fellowship from the Jacobs Foundation to study the association between sleep and memory consolidation in children. In 2018, Mara Mather from the University of Southern California was awarded the Max Planck Sabbatical Award, which provides renowned scientists with dedicated grant support to foster collaboration with the hosting Max Planck Institute. This award has allowed Mara Mather and researchers of the RHYME project to deepen their collaboration on the locus coeruleus and noradrenergic neuromodulation as a prime driver of adult age differences in episodic memory (Dahl et al., 2019). In 2019, Elliot Tucker-Drob from the University of Texas at Austin received the Max-Planck-Humboldt Medal for his contributions to lifespan psychology. The medal is given to researchers with outstanding future potential who intend to collaborate with colleagues at a research institution in Germany. In the years to come, Elliot Tucker-Drob, who is an alumnus of the International Max Planck Research School on the Life Course (IMPRS LIFE) at the University of Virginia, will collaborate with Andreas Brandmaier and Ulman Lindenberger to develop multivariate methods that afford causal inferences about mechanisms that underlie individual differences in behavioral development across the lifespan.

Overview of Research Projects at the Center for Lifespan Psychology

Currently, in March/April 2020, empirical and conceptual work at the Center is structured into eight research projects (see Table 1). Compared to the 2014–2016 reporting period, the former project, *Cognitive and Neural Dynamics of Memory Across the Lifespan* (ConMem), was split into two projects, RHYME and LIME, to accommodate its growing size and within-project specialization. At the same time, the former project *Intra-Person Dynamics Across the Lifespan* was merged with the project *Formal Methods in Lifespan Psychology,* reflecting the high degree of overlap between the two.

The activities pursued in these eight projects cover a wide array of research areas in human behavioral development. For example, the following questions have been addressed during the reporting period: (a) How can we design and implement data analysis workflows that ascertain the reproducibility of the results we report in our empirical publications (cf. pp. 295 f.)? (b) Is there a link between the precision of slow oscillation-spindle coupling during slow-wave sleep and memory consolidation in younger and older adults (Muehlroth, Sander et al., 2019)? (c) Do structural aspects of hippocampal subfields and limbic white matter predict individual differences in the learning rate among older adults (Bender et al., 2020)? (d) If the true shape of longitudinal change is exponential, but our analysis tools assume linearity, are researchers likely to notice the discrepancy in the context of standard longitudinal research designs (Ghisletta et al., 2020)? We provide our current answers to these questions and many more on the following pages.

Table 1. The Center for Lifespan Psychology at the Max Planck Institute for Human Development: Overview of Research Projects

Name of Project	*Researchers, Including Postdoctoral Fellows*	*Predoctoral Research Fellows*
Lifespan Neural Dynamics Group (LNDG; cf. pp. 195 ff.)	Douglas D. Garrett**; Niels A. Kloosterman*, Kristoffer N. T. Månsson*, Leonhard Waschke*, Iris Wiegand*	Julian Q. Kosciessa, Liliana Polyanska, Alexander Skowron
Lifespan Rhythms of Memory and Cognition (RHYME)	Markus Werkle-Bergner**; Martin J. Dahl*, Ulman Lindenberger, Chi (Zoe) Ngo*	Elisa S. Buchberger, Ann-Kathrin Jöchner, Beate E. Mühlroth
Lifespan Age Differences in Memory Representations (LIME)	Myriam C. Sander[1]**; Ulman Lindenberger	Anna Karlsson, Malte Kobelt°, Claire Pauley, Verena R. Sommer
The Berlin Aging Studies (BASE & BASE-II)	Julia A. M. Delius**, Sandra Düzel**; Andreas Brandmaier, Ylva Köhncke*, Ulman Lindenberger, Mara Mather°, Gert G. Wagner[2]	Sarah Polk
Mechanisms and Sequential Progression of Plasticity	Yana Fandakova**, Elisabeth Wenger**; Maike M. Kleemeyer*, Corinna Laube*, Ziyong Lin*, Ulman Lindenberger	Neda Khosravani, Eleftheria Papadaki
Interactive Brains, Social Minds	Viktor Müller**; Ulman Lindenberger	
Brain Imaging Methods in Lifespan Psychology	Nils C. Bodammer**; Ulman Lindenberger, Naftali Raz, Davide Santoro	
Formal Methods in Lifespan Psychology	Andreas M. Brandmaier**; Marie K. Deserno*, Charles C. Driver, Maike M. Kleemeyer*, Ylva Köhncke*, Ulman Lindenberger, Timo von Oertzen°	Manuel Arnold°

Note. Head of Research Planning and Research Coordination: Imke Kruse. The table refers to projects and project members as of March/April 2020; for updates, visit www.mpib-berlin.mpg.de.
**Principal investigator; *Postdoctoral fellow; °Primary affiliation with another institution.
[1] Myriam C. Sander leads a Minerva Research Group.
[2] Gert G. Wagner is Max Planck Fellow at the MPI for Human Development (see pp. 253 ff. for more information).

Research Project 1: Lifespan Rhythms of Memory and Cognition (RHYME)

Research Scientists

Markus Werkle-Bergner

Martin J. Dahl
Attila Keresztes
(until 11/2018)
Beate E. Mühlroth
Chi (Zoe) Ngo
(as of 09/2019)

Elisa S. Buchberger
(as of 10/2019)
Ann-Kathrin Jöchner
(as of 01/2018)

This project investigates lifespan changes in attention, working memory, and episodic memory at structural, functional, and behavioral levels of analysis, with an emphasis on age differences in the coordination of oscillatory brain activity. It combines experimental with longitudinal research designs and uses multimodal data from a wide range of neuroimaging methods. During the reporting period, the project's research activities were centered around four interrelated themes.

Aging Cognition, Neuromodulation, and Rhythmic Neural Activity

In their daily lives, individuals constantly experience a wide range of feelings, thoughts, and sensations. To permit goal-directed behavior and sustain cognitive development, some of these signals need to be enhanced whereas others need to be suppressed. At the neural level, this selection operation is implemented by a network of frontoparietal cortical regions, interconnected via the thalamus. Processing in this network is orchestrated through temporally synchronized activation patterns. Neuromodulators are of key importance in this process, as they regulate the efficacy of synaptic transmission. We hypothesize that senescent changes in the precision with which neuromodulators are released from brainstem nuclei might affect the functionality of selective processing, rendering selection more difficult with advancing adult age.

In a series of studies (Dissertation Martin J. Dahl) conducted in collaboration with Mara Mather from the University of Southern California, USA, we have probed the interaction between age-associated differences in the integrity and functionality of the central noradrenergic system and rhythmic neural activity in the alpha frequency range (~10 Hz). Structurally, we focused on the locus coeruleus (LC), a small brainstem nucleus that serves as the main source of norepinephrine (NE) in the brain. In the past, the LC's small size and location deep in the brain have prevented noninvasive studies of its integrity and functionality. Hence, in a first study (Dahl, Mather et al., 2019), we developed a semiautomatic method to derive individualized estimates of structural LC integrity from high-resolution neuromelanin-sensitive magnetic resonance images (MRI; see Figure 5). Applying these methods in samples of younger and older adults from the Berlin Aging Study II (see also pp. 138 ff.), we found that LC integrity correlated positively with individual differences in learning and memory across age groups and within the group of older adults. Analyses across the rostro-caudal extent of the LC revealed spatially confined and functionally relevant age differences in LC integrity. Critically, older adults who showed more youth-like intensity ratios in rostral, hippocampus (HC)-projecting LC segments also showed higher levels of memory performance. An LC probability map derived from this study is freely available to the neuroscience community to facilitate comparability of studies.

Memory is tightly modulated by attention, but the contribution of adult age differences in attention to memory is not well understood. To reveal the interplay between the functionality of the NE system and rhythmic neural activity in the alpha frequency range that modulates attention, we used neuromelanin-sensitive MRI, pupillometry, and electroencephalography (EEG) to relate the structural and functional integrity of the central NE system to rhythmic neural activity in the context of a demanding auditory selective attention task. Recently, we used the same task to reveal a partial reorganization of attention-related rhythmic neural responses (Dahl, Ilg et al., 2019). We combined the auditory attention task with a fear-conditioning manipulation to manipulate NE release on a trial-by-trial level. During conditioning trials, we noted a reliable arousal response reflected in larger pupil responses and stronger desynchronization of rhythmic neural alpha activity for trials with the reinforced conditioned stimulus (CS+) compared to non-reinforced (CS–) trials. Critically, presentation of fear-conditioned stimuli during the auditory

Key References

Dahl, M. J., Ilg, L., Li, S.-C., Passow, S., & **Werkle-Bergner, M**. (2019). Diminished pre-stimulus alpha-lateralization suggests compromised self-initiated attentional control of auditory processing in old age. *NeuroImage, 197,* 414–424. https://doi.org/10.1016/j.neuroimage.2019.04.080

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Link to LC Map
www.mpib-berlin.mpg.de/lc-map

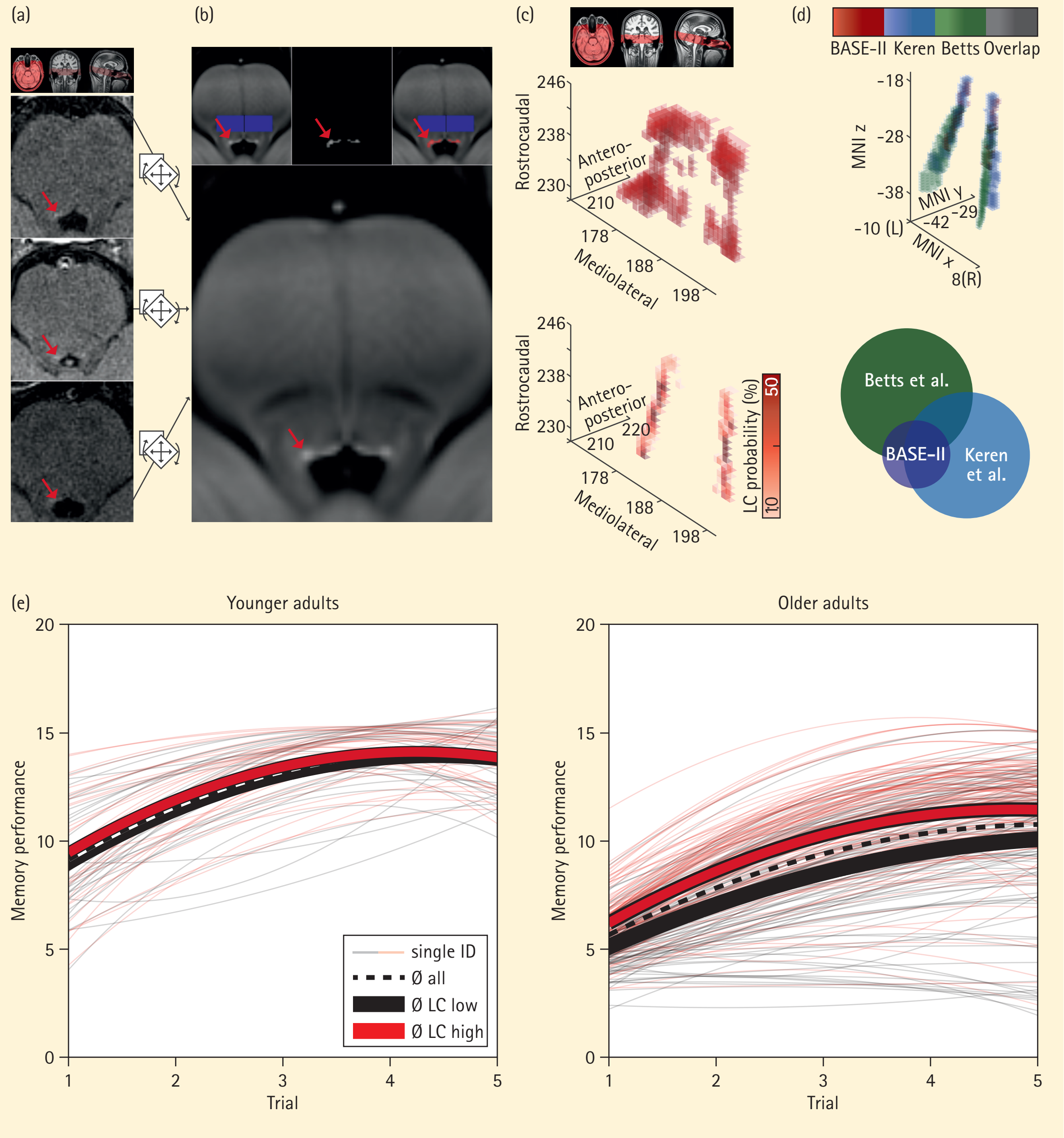

Figure 5. Schematic overview of the semiautomatic analysis procedure developed to extract individual locus coeruleus (LC) intensity values across the rostrocaudal extent. (a) Native-space neuromelanin-sensitive brainstem scans of three randomly selected participants (axial slices are shown). Hyperintensities corresponding to the LC are indicated by red arrows. (b) Neuromelanin-sensitive scans were aligned and pooled across participants to increase the signal-to-noise ratio and to facilitate LC delineation using a template-based approach. On a group level, LC location (red) was semiautomatically determined based on an intensity threshold relative to a pontine reference area (blue; see inlays). (c) Areas surviving the thresholding were grouped into a volume of interest (search space: upper plot; 3D representation) and used to restrict automatized extraction of individual peak intensities and their location. Observed peak LC locations were converted to a LC probability map (lower plot). (d) In standard space, the LC probability map was successfully validated using previously published maps. Circle radius indicates map size (i.e., number of voxels). (e) Estimated learning and memory performance trajectories for younger and older adults. To enable visualization of the association between LC integrity and memory performance, single participants (thin lines; ID) are color-coded based on LC integrity (median-split), and mean trajectories for subgroups are displayed (thick lines). Left: $n = 33$ younger adults in the low- and high-LC groups respectively; right: $n = 114$ older adults each in the low- and high-LC groups, respectively (adapted from Dahl, Mather et al., 2019).

Key Reference

Muehlroth, B. E., Sander, M. C., Fandakova, Y., Grandy, T. H., Rasch, B., Shing, Y. L., & **Werkle-Bergner, M.** (2020). Memory quality modulates the effect of aging on memory consolidation during sleep: Reduced maintenance but intact gain. *NeuroImage, 209,* Article 116490. https://doi.org/10.1016/j.neuroimage.2019.116490

attention task reinstated the acquired arousal response in the absence of reinforcements. When combining the behavioral and physiological data in a structural equation model, we found that a more responsive noradrenergic system was associated with more proficient attention performance and that older adults showed a reduced responsiveness of the NE system relative to young adults (Dahl et al., 2020).

Taken together, these findings indicate that reduced structural integrity and functional responsiveness of the central noradrenergic system is associated with age differences in attention and memory. Specifically, our multimodal data suggest that age-related changes in noradrenergic neuromodulation might affect attention and memory through alterations in low-frequency rhythmic neural activity.

The Co-Development of Brain, Sleep, and Cognition

Sleep, like breathing, arguably belongs to the most basic bodily needs. Healthy sleep supports learning and memory, whereas lack of sleep hinders knowledge acquisition. After a day full of learning, sleep supports the stabilization and integration of experiences into a framework of personal memories while setting the stage for continued learning during ensuing wakefulness.

Thus far, most research into the causes of memory decline during adulthood and old age has focused on the encoding of new and the retrieval of previously acquired experiences. However, the long-term maintenance of new experiences also requires consolidation, defined as the stabilization of memory representations beyond initial encoding. According to the Active System Consolidation framework introduced by Jan Born and colleagues, sleep plays a central role in consolidation by facilitating interactions between fast-learning HC and slow-learning cortical systems.

Normal human aging entails fundamental changes in sleep and brain structure, even in the absence of pathology. To date, only few studies have attempted to unravel age differences in sleep physiology, brain structure, and memory consolidation. In part, this lack of relevant research reflects methodological problems when attempting to compare this triad across age groups.

In collaboration with Björn Rasch (University of Fribourg, Switzerland), we conducted a large age-comparative study on the influence of memory quality on encoding, consolidation, and retrieval (Dissertation Beate E. Mühlroth). The study consisted of a multisession protocol including behavioral, EEG, and MRI assessments, as well as ambulatory polysomnographic sleep monitoring. Healthy younger and older adults worked on an age-adapted associative memory task for two consecutive days. The task was developed to assess memory strength at the single-item level within each study participant. We aimed at disentangling the effects of reduced overnight forgetting from active enhancement of initially labile memory traces.

A first set of analyses targeted two main questions: first, whether age differences in sleep-dependent consolidation depend on the quality of memory representations formed during learning; and second, whether individual differences in sleep physiology and brain structure predict differences in consolidation within and across age groups (see Muehlroth, Sander et al., 2020). As expected, age differences in sleep-dependent memory stabilization were most pronounced at medium levels of encoding quality. Partial least squares (PLS) analyses identified differences in sleep physiology and brain structure that were associated with older age. However, when selecting younger and older adults based on their similarity in sleep physiology and brain structure, as reflected in the PLS scores, neither of the two in isolation was sufficient to account for age differences in consolidation (see Figure 6).

We next sought to better understand what might drive the observed age differences in sleep-dependent consolidation. Active System Consolidation theory suggests that the transfer of labile HC-dependent representations into more stable cortical networks critically depends on the precise temporal coordination of cortical slow oscillations (SO) with fast-frequency thalamo-cortical spindles (Sp). Accordingly, animal research indicates that precise SO–Sp coupling is critical for consoli-

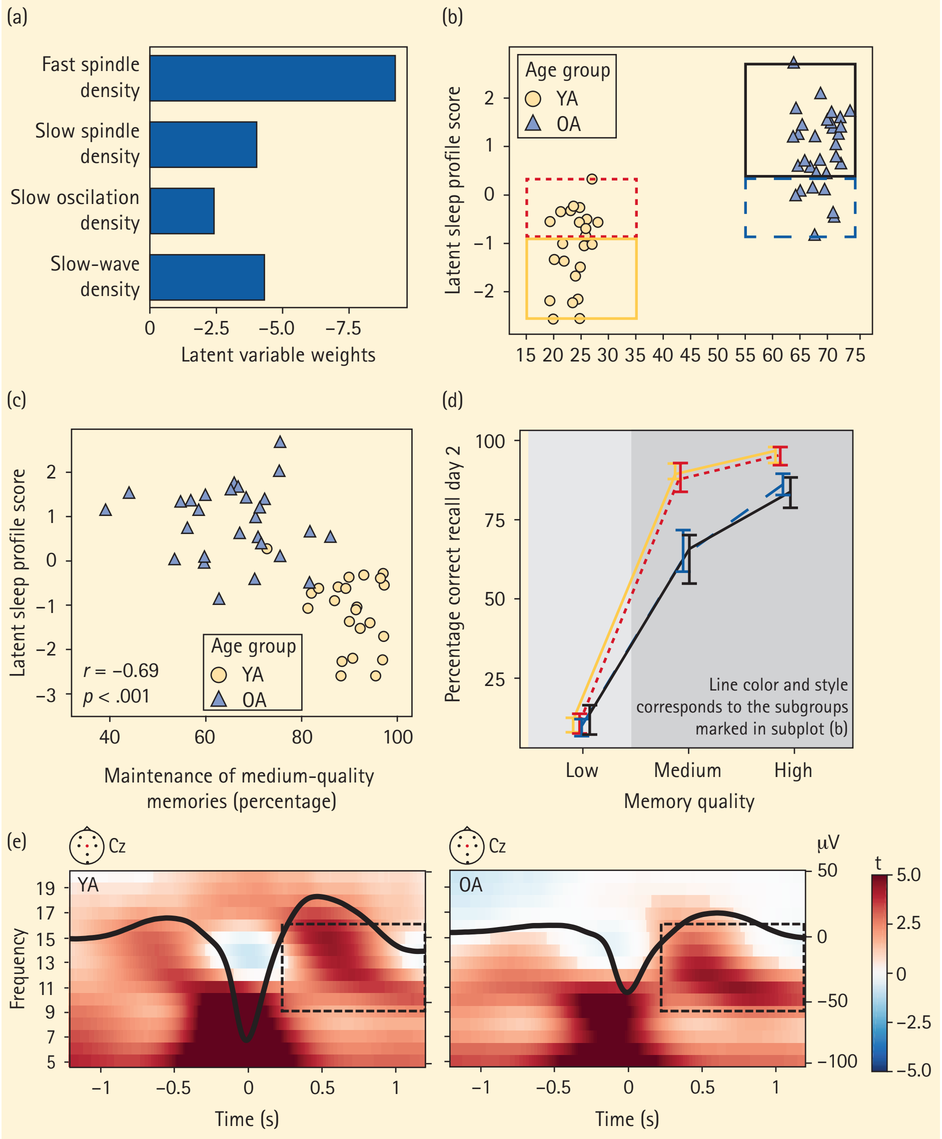

Figure 6. Sleep–memory associations in younger and older adults (adapted from Muehlroth et al., 2019, 2020). (a) Partial-least-squares solution relating physiological sleep indicators to age. The resulting latent variable captures the common variance between participants' age and sleep. Latent variable weights (in *Z*-scores) demonstrate that all physiological sleep indicators have a stable negative relation to age. (b) Each participant's expression of the latent variable is plotted against age. Overlap between the age groups is marked by dashed boxes. (c) Each participant's latent sleep-profile score is plotted as a function of memory performance. Spearman's rank-order correlation coefficients for the whole sample are displayed. Maintenance of medium-quality memories relates to the latent sleep-profile score across age groups. (d) Median behavioral performance for all subgroups is displayed, with grouping, line color, and style corresponding to (b). The first and third quartiles are depicted as error bars. Memory gain (shaded in light gray) is similar in all subgroups. Memory maintenance (shaded in darker gray) is modulated by sleep profile, but differs between younger and older adults even when they have the same sleep profile. (e) Age differences in slow-oscillation-spindle coupling (Muehlroth et al., 2019). Differences in wavelet power for slow-oscillations (SO) trials (respective down peak ± 1.2 s) compared to trials without SOs are depicted (in *t*-score units). The average frontal SO for each age group is inserted in black (the scale in μV is indicated on the right of each time–frequency graph). In both age groups, EEG power is modulated as a function of the SO phase. In younger adults (on the left), fast spindle activity (12–15 Hz) peaks during the up peak of the SO. Slow spindle power (9–12 Hz) is strongest at the up- to down-state transition. In older adults (on the right), power increases are delayed and shifted to lower frequencies as compared to younger adults.
YA: younger adults; OA: older adults.

Key Reference

Muehlroth, B. E., Sander, M. C., Fandakova, Y., Grandy, T. H., Rasch, B., **Shing, Y. L., & Werkle-Bergner, M.** (2019). Precise slow oscillation-spindle coupling promotes memory consolidation in younger and older adults. *Scientific Reports, 9*, Article 1940. https://doi.org/10.1038/s41598-018-36557-z dation. Most studies in humans thus far have looked at the contributions of each of the two components, but not at the precision of their coupling.

We used individually adjustable detection algorithms to identify individual SO and Sp events (see Muehlroth et al., 2019). On that basis, we were able to show that less precise coupling between slow waves and spindles is indeed associated with lower overnight memory maintenance among older adults. In addition, older adults with greater structural integrity of brain regions relevant for sleep and memory were more likely to show precise coupling patterns resembling those of younger adults than older adults with lower brain integrity.

In sum, this line of research suggests that age differences in sleep-associated consolidation depend on the precise coupling among cardinal neural sleep rhythms supported by the integrity of relevant brain structures.

Research on sleep and aging has sought to develop new approaches to identify and possibly treat age-associated pathological conditions. In particular, attempts to establish sleep as a novel biomarker and treatment target for Alzheimer's disease have led to a growing interest in research on sleep and aging. This rise in interest has not been matched by a careful scrutiny of data-analytic procedures.

In a theoretical and empirical analysis (Muehlroth & Werkle-Bergner, 2020), we used electrophysiological sleep and structural brain data of healthy younger and older adults to identify, illustrate, and resolve methodological core challenges in the study of sleep and aging. We demonstrated potential biases in common analytic approaches when applied to heterogeneous populations, especially regarding markers of rhythmic neural activity during sleep. Using empirical demonstrations, we show that uncovering age-dependent alterations in the physiology of sleep requires the development and use of age-group adjusted and individualized data-analytic procedures. Ultimately, these innovations may yield valid and reliable biomarkers that discriminate between normal and pathological age-related changes in sleep physiology.

A key challenge for the age-adapted analysis of rhythmic neural activity—like sleep oscillations—is the identification of individual rhythmic events and their separation from arrhythmic background activity. In collaboration with the Lifespan Neural Dynamics Group (see also pp. 195 ff.), we extended and improved an existing rhythm detection method (Kosciessa et al., 2020; see also p. 199 for further details).

Development of Memory Specificity and Intra-Hippocampal Maturation

At the other end of the lifespan, the project has begun to link HC maturation to memory development. Just as any other adaptive learning system, children are confronted with two conflicting goals. They need to detect regularities in the world through generalization while remembering specific events through disambiguation. Core aspects of these functions are implemented in the internal neural circuits of the HC. Animal studies suggest that HC subfields reorganize during maturation. Studying this reorganization in the human HC is technically challenging. As a result, the ontogenetic timing of HC maturation is controversial, and its contribution to generalization and specificity in cognitive development remains elusive. In a study using high-resolution in-vivo MRI data from children (6–14 years old) and younger adults (Keresztes et al., 2017), we were able to identify a multivariate profile of age-related differences in intra-HC structures and to show that HC maturity as captured by this pattern is associated with age differences in the differential encoding of unique memory representations. The uneven time course of HC subfield maturation identified in this study provides a mechanistic explanation for the observation that generalization precedes specification in memory development during childhood (for a theoretical overview, see Keresztes et al., 2018).

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Muehlroth, B. E., & **Werkle-Bergner, M.** (2020). Understanding the interplay of sleep and aging: Methodological challenges. *Psychophysiology, 57*(3), Article e13523. https://doi.org/10.1111/psyp.13523

Research Project 2: Lifespan Age Differences in Memory Representations (LIME)

LIME investigates mechanisms of memory formation, consolidation, and retrieval, with a focus on the ways in which these mechanisms change across the lifespan (see Sander et al., 2012). The project addresses the fundamental question whether aging-induced decrements in the distinctiveness of neural representations contribute to age-related losses in memory performance during adulthood and old age. Providing answers to this question requires the coordination of concepts and methods from lifespan psychology, cognitive neuroscience, and computational neuroscience. Accordingly, the project relies on experimental research designs, advanced multimodal imaging methods, and computational modeling. The project continues and broadens the work of Myriam Sander's Minerva Group, which was established in 2016.

Research Area 1: Age Differences in Similarity and Distinctiveness of Memory Representations

Are memories represented differently in older than in younger adults? According to the dedifferentiation hypothesis, age-related cognitive decline during adulthood and old age reflects decrements in the distinctiveness of neural representations and processing pathways (Li et al., 2001). In line with this hypothesis, pioneering work by Denise Park and colleagues has shown that differences in the neural representation between items belonging to different categories, such as houses and faces, are less pronounced in older adults than in younger adults. However, most studies thus far have not yet linked differences in the distinctiveness of individual memory representations to adult age differences in cognitive performance. In the LIME project, we systematically probe whether links between neural distinctiveness and performance help to elucidate adult age differences in episodic memory.

In pursuing this research question, the project makes ample use of subsequent memory paradigms, which analyze recall success as a function of neural activity during encoding, such as variations in oscillatory power measured with electroencephalography (EEG). In particular, power increases in the theta band accompanied by power decreases in the alpha/beta bands have been shown to indicate associative binding and elaboration mechanisms in young adults. We were able to show that these oscillatory mechanisms of successful memory formation remain relevant in old age (Sander et al., 2020; see Figure 7).

In addition, multimodal analyses revealed a clear structure–function relationship between the integrity of memory-related brain regions and the strength of the oscillatory subsequent memory effect. In particular, older adults' lower structural integrity of the inferior frontal gyrus (IFG), a region known to be involved in elaboration processes, was accompanied by reduced subsequent memory effects in the alpha frequency. Taken together, these results indicate that memory representations tend to be formed with fewer details with advancing adult age (Sander et al., 2020), with downstream consequences for long-term maintenance and forgetting (see Fandakova et al., 2020).

Recent results from another study support the hypothesis that older adults form less detailed representations than younger adults. Using representational similarity analysis, we compared the similarity of spatiotemporal EEG frequency patterns during initial encoding in relation to subsequent recall performance in younger and older adults (Dissertation Verena Sommer; Sommer et al., 2019). Specifically, we addressed the question whether successful memory is reflected in relatively more distinct or relatively more similar patterns of neural activity in younger and older adults. We found that the association between memory success and pattern similarity differed between young and older adults, suggesting age differences in basic cognitive encoding processes. For older adults, better memory performance was linked to higher similarity during early stages of encoding. For younger adults, lower similarity during later periods of encoding was positively related to memory performance

Research Scientists

Myriam C. Sander

Ulman Lindenberger
Claudia Wehrspaun
(until 03/2019)

Anna Karlsson
(as of 03/2017)
Malte Kobelt
(guest, 04/2019–04/2020)
Verena R. Sommer

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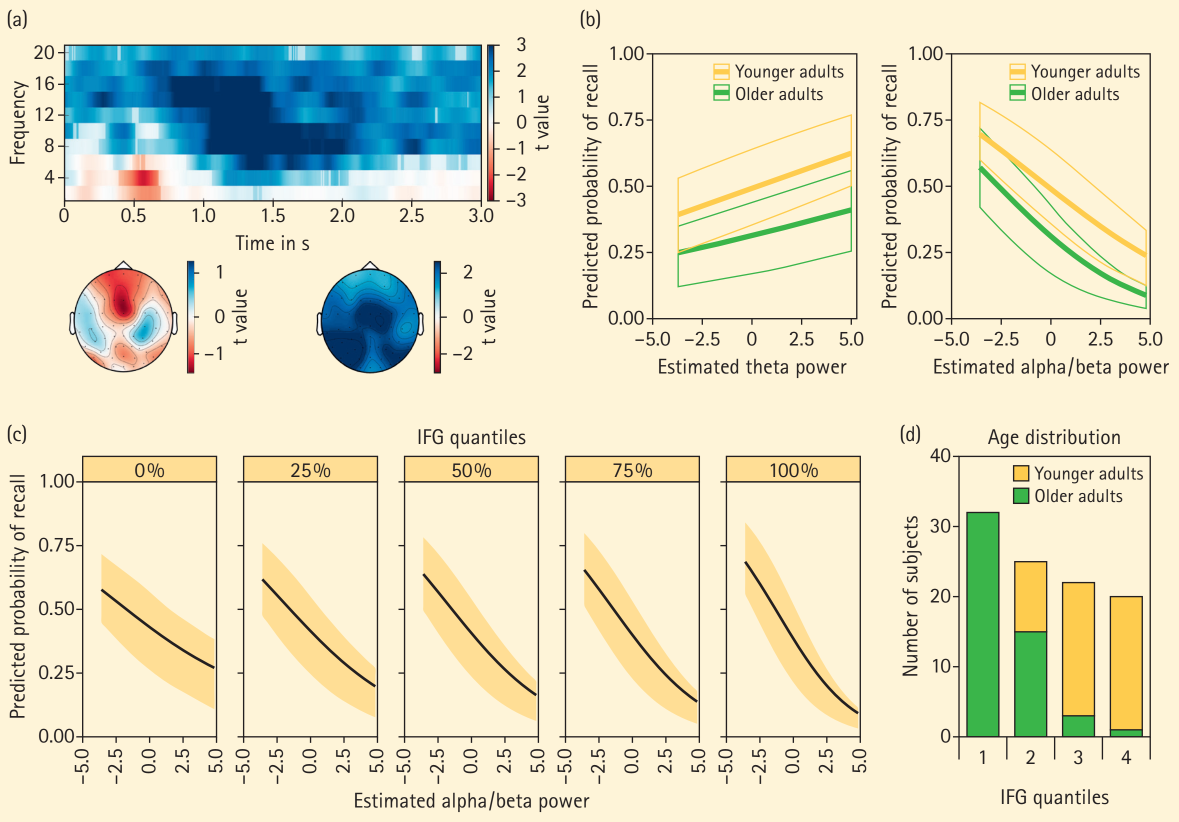

Figure 7. (a) Time-frequency plot of subsequent memory effects (thus, the difference in power of recalled vs. not-recalled word pairs) in theta and alpha/beta power, collapsed across age groups. (b) Power modulations in theta (left) and alpha/beta (right) frequencies predict single trial accuracy in both younger and older adults. (c) Alpha/beta band power is more predictive for memory recall in participants with high cortical thickness of the inferior frontal gyrus (IFG) than in those with lower cortical thickness, as shown by displaying predicted probabilities of varying alpha power for IFG quantiles. (d) Distribution of older and younger adults across different levels of structural integrity of the IFG (represented by quantiles). Most of the participants with low cortical thickness are older, indicating that reduced memory performance in older adults can be attributed to lower structural integrity of the IFG, which is related to smaller subsequent memory effects in alpha/beta power (adapted from Sander et al., 2020).

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Key Reference

Sander, M. C., Fandakova, Y., Grandy, T. H., Shing, Y. L., & Werkle-Bergner, M. (2020). Oscillatory mechanisms of successful memory formation in younger and older adults are related to structural integrity. *Cerebral Cortex.* Advance online publication. https://doi.org/10.1093/cercor/bhz339

(see Figure 8). These results suggest that older adults rely more on encoding the general gist of stimuli, reflected in increased early encoding similarity, whereas young adults tend to form and encode mental images with distinct details, reflected in increased dissimilarity during later phases of encoding.

In our ongoing studies, we take a closer look at adult age differences in representational patterns. In a recent functional magnetic resonance imaging (fMRI) paradigm, we went beyond the mass-univariate characterization of neural specificity at the category level, and instead used representational similarity analyses to relate memory performance differences between age groups to neural pattern stability across repeated exposures, and to neural pattern similarity of different exemplars within one semantic category relative to the similarity of objects from different categories. Initial analyses suggest that the stability or self-similarity of neural representations at the item level, relative to their similarity to other items of the same category, is negatively related to adult age and positively related to memory performance.

Adaptation paradigms offer yet another approach to probe the specificity of representations. These paradigms rest on the assumption that neuronal populations reduce their responses (i.e., adapt) when stimulus features to which they are sensitive are repeated.

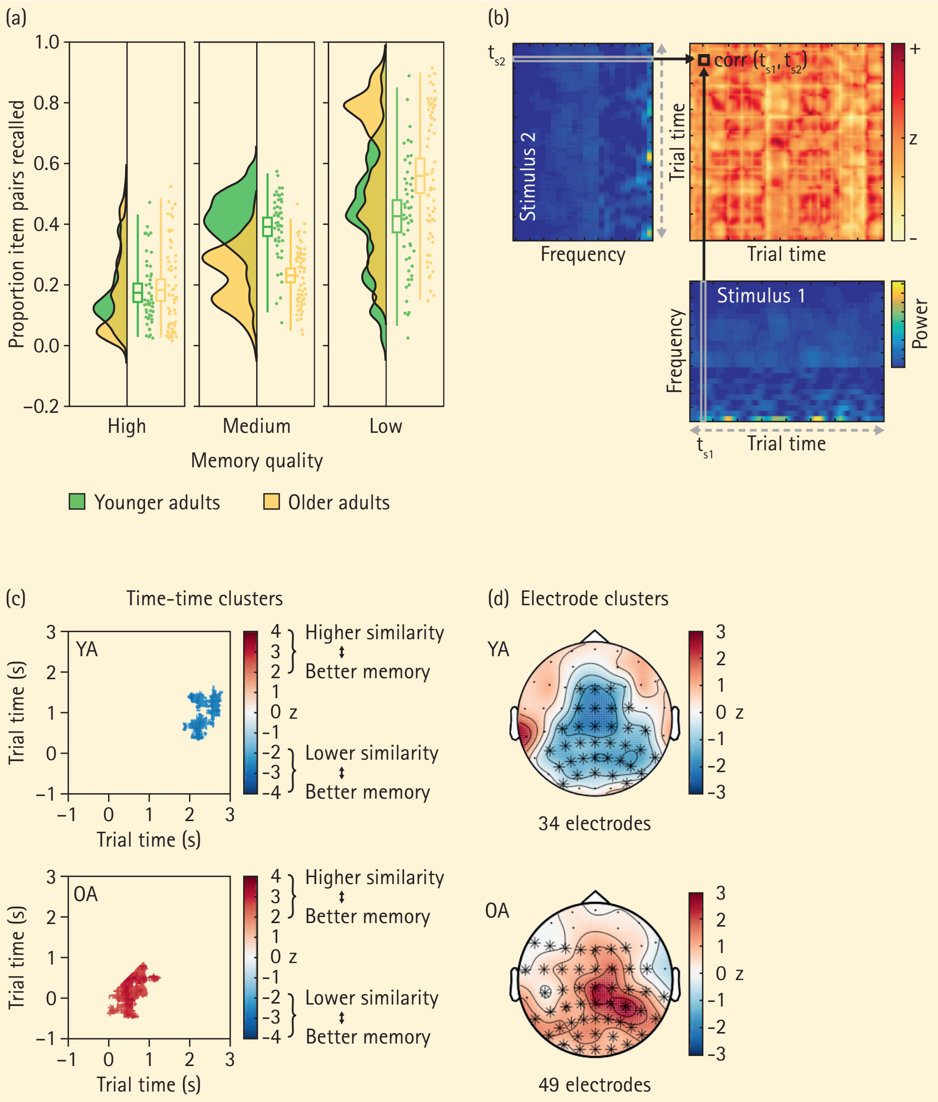

Figure 8. (a) Age differences in the quality of memory representations. In this study, participants repeatedly studied word–scene pairs followed by several rounds of cued recall. The quality of memory representations was defined by the fate of the individual pair across the course of the experiment. The figure shows the proportion items with high, medium, and low memory quality for young adults (YA) and older adults (OA). Older adults have a lower proportion of medium-quality and a higher proportion of lower-quality items than younger adults. (b) Spectral representational similarity analysis methodology. Frequency vectors from every time point of stimulus 1 are Pearson-correlated with frequency vectors from every time point of stimulus 2 (corr(t_{s1}, t_{s2})) resulting in a time-time similarity matrix representing the similarity of the frequency patterns of these two stimuli at all possible time-time combinations at one electrode. (c) Time-time clusters with the corresponding topography (d) in which the stimuli of different memory quality reliably differed from another in each age group. Whereas higher similarity in an early (positive) cluster is related to a higher recall probability in older adults, higher distinctiveness (negative cluster) is beneficial for memory performance in younger adults (adapted from Sommer et al., 2019).

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The magnitude of adaptation is thus a direct measure of representation specificity. In a lifespan EEG study, we investigated whether differences in adaptation magnitudes predict differences in memory performance between children, young adults, and older adults (Dissertation Verena Sommer). To this end, we varied the number of exposures and the degree of similarity to other stimuli of visually presented objects. Event-related potentials displayed adaptation effects in all age groups and were associated with memory specificity. Our findings demonstrate that adaptation effects reflect encoding mechanisms that facilitate the formation of stimulus-specific memory representations, again highlighting their significance as neural indicators of individual differences in episodic memory across the lifespan. The extension of this investigation to child development was accomplished in collaboration with Sarah Weigelt (formerly Ruhr-Universität Bochum, now Technische Universität Dortmund).

Research Area 2: Effects of Context on Memory Representations

Successful memory is greatly aided by the spatial and temporal settings of an event, commonly referred to as its context. This dependency of memory on context increases with advancing adult age (Lindenberger & Mayr, 2014). At the same time, and somewhat paradoxically, older adults find it particularly difficult to actively retrieve specific object–context associations. Based on these observations, our studies aim at a better understanding of age differences in the contextualization of memories and the precise conditions under which memory performance benefits from context reinstatement.

In a large multimodal study that combined EEG, functional and structural MRI, and eye tracking, we have been investigating how context shapes younger and older adults' memories for objects (Dissertation Anna Karlsson; see Figure 9a). We established a high-resolution multiband fMRI sequence that will allow us to track functional activations at the level of hippocampal subfields. So far, our behavioral results support the well-known observation of lower pair memory performance in older adults compared to younger adults, with no age group differences in object memory. For object memory performance, context reinstatement was beneficial in both age groups, and seeing an object in both a familiar and a new context impaired performance. However, pair memory was only reduced when participants saw an object in a familiar, incorrect context, but not with a new context. These results suggest different contributions of familiarity and novelty detection for object and pair memory (see Figure 9b). Our electrophysiological results suggest that power modulations during encoding, as indicated by subsequent memory effects in alpha/beta band and theta band power measured with EEG, predict single-trial accuracy for both objects and object–context pairs. Interestingly, alpha/beta desynchronization was modulated by both context condition and age group. Larger desynchronization was related to a larger beneficial effect of context for pair memory when the context was old as compared to familiar, and more so in younger than in older adults. This result suggests that younger adults' deeper elaboration during encoding is a way to establish a reliable representation of the object–context pair that comes with a higher probability of recall. We are currently following up on these findings by investigating learning-related changes in neural patterns of object-specific representations in the hippocampus as captured by fMRI.

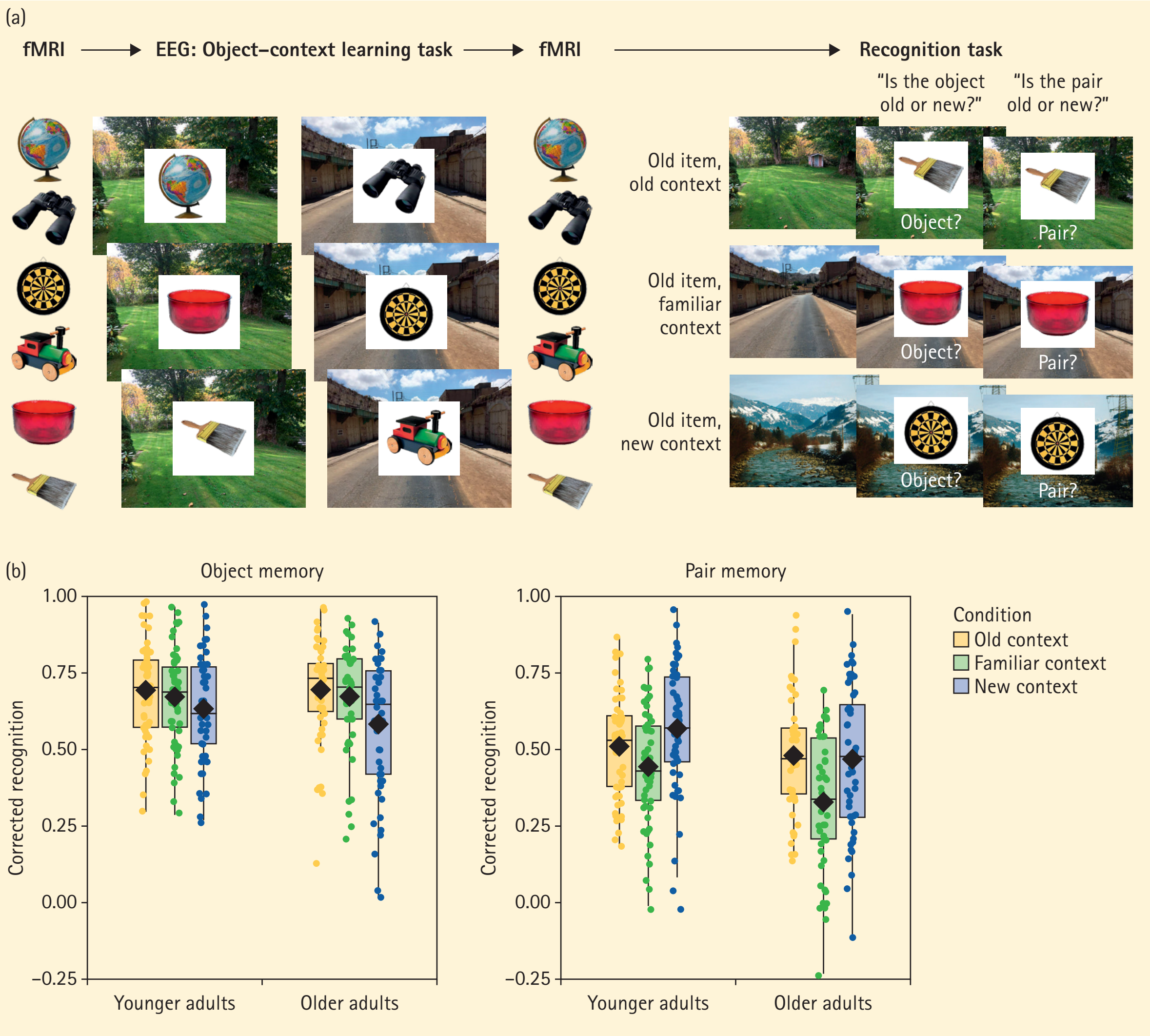

Figure 9. (a) Experimental paradigm of the multimodal study that combined EEG, functional MRI, and structural MRI to investigate the effect of context on memory (Dissertation Anna Karlsson). Participants were first familiarized with pictures of objects in the scanner to measure object-specific activation patterns. The main experiment consisted of an object–context learning paradigm during which EEG was assessed. This was followed by a postlearning fMRI measurement intended to reveal changes in memory representations. Finally, participants took a recognition memory test in which objects were presented with either the original learning context, a familiar context, or a new context. We first tested their memory for the object, followed by the question whether the object–context pair was the same as during learning. (b) First behavioral results: Corrected recognition scores (hits minus false alarms) for the different context conditions (old/familiar/new) as a function of age for object memory (left) and pair memory (right). Age groups differ when the retrieval of object–context pairs is required, but not when only objects need to be recalled. Context reinstatement (original context) benefits performance in both age groups, and seeing an object with a familiar, but incorrect context impairs performance.

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Research Scientists

Julia A. M. Delius
Sandra Düzel

Caroline Beese
(as of 05/2019)
Andrew R. Bender
(until 01/2018)
Andreas M. Brandmaier
Maike M. Kleemeyer
(as of 09/2019)
Ylva Köhncke
(as of 07/2017)
Ulman Lindenberger

Sarah Polk
(as of 04/2019)

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Research Project 3: The Berlin Aging Studies (BASE & BASE-II)

In the course of the 20th century, average life expectancy almost doubled. More and more individuals will experience additional years of life between the ages of 70 and 100+. What do these added years mean in terms of functional capacity and quality of life? And how do the years and months preceding death in old age differ from the years before? In concert with other longitudinal studies, the Berlin Aging Studies provide a basis for answering questions of this sort. The specific focus of the BASE project at the Center for Lifespan Psychology is on cognitive, psychosocial, and methodological aspects in the study of human aging.

For more than three decades, members of the Center have been investigating age- and death-related changes in psychological functioning in the context of the Berlin Aging Study (BASE; Baltes & Mayer, 1999; Lindenberger et al., 2010) and the Berlin Aging Study II (BASE-II; Demuth et al., 2019). Both studies are highly collaborative and multidisciplinary, involving researchers from institutions inside and outside Berlin. The two studies also take part in the Lifebrain consortium, which is funded under the European Union Horizon 2020 Framework Programme (Walhovd et al., 2018; cf. p. 139).

The Berlin Aging Study (BASE)

Longitudinal data in BASE are available for eight measurement occasions spanning more than 18 years, and mortality-related information has been updated at regular intervals. Mrs. A. was one of the 516 individuals who started participating in BASE almost 30 years ago. After having participated in all of the seven measurement occasions that followed the initial assessment, she died in December 2019 at the age of 107. As Figure 10 shows, she led an active life in her own home until a fall forced her to move into a nursing care institution about three months before her death. Additional biographical data reveal what a remarkable person she was (see Figure 11). Her life history reminds us that the data we analyze are greatly abstracted and impoverished representations of real people. As in previous years, the BASE data have continued to provide the basis for new original publications on individual differences in late-life development (e.g., Mueller et al., 2018).

Figure 10. BASE participant Mrs. A., aged 106, at her home during a visit by BASE colleagues Denis Gerstorf and Sandra Düzel in 2018.

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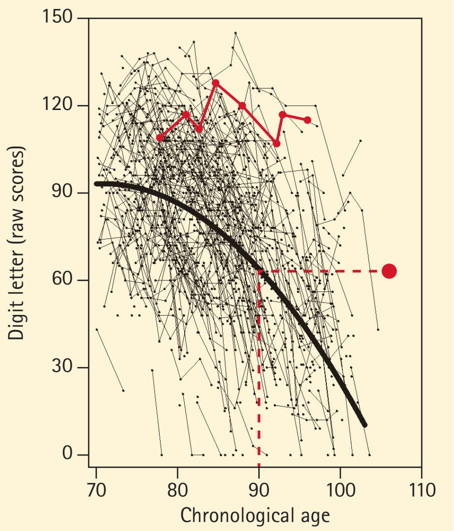

Figure 11. BASE participants' score trajectories in the Digit Letter test, with Mrs. A.'s scores highlighted in red. At the age of 106 (larger dot), her score was still at the level of the average 90-year-old BASE participant.

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The presence of similar or identical measures in BASE and BASE-II (see below) allow for estimates of cohort differences in various aspects of normal aging, such as control beliefs (Gerstorf et al., 2019) and cardiovascular health (König et al., 2018). The results from these studies document the extent to which societal changes can influence the course of normal aging in desirable directions within relatively short periods of time.

The Berlin Aging Study II (BASE-II)

The Psychology Unit of BASE-II aims at obtaining a comprehensive picture of age-related differences and changes in brain and behavior. In search of mechanistic explanations for individual differences in normal aging, we use advanced statistical modeling techniques to investigate the impact of risk factors, such as metabolic syndrome and loneliness, and protective factors, such as physical activity.

Adults' brains differ reliably in the onset and degree of age-related volume losses. Age-related changes in cognition have been associated with differences in structural brain parameters, including cerebral white matter (WM) microstructure, hippocampal (HC) volume, as well as the integrity of neurotransmitter systems such as the locus coeruleus. By combining newly developed semiautomatic analysis procedures to assess HC subfield volumes with structural equation modeling techniques, Bender et al. (2020) found that structural characteristics of limbic WM regions and HC volume jointly contribute to verbal learning in older adults. Moreover, rates of shrinkage of brain regions and cognitive changes were exacerbated by hypertension and metabolic syndrome. Düzel, Buchmann et al. (2018) used structural equation modeling to set up a latent factor of metabolic load that was associated with indicators of physical health in both men and

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Düzel, S., Buchmann, N., Drewelies, J., Gerstorf, D., **Lindenberger, U.,** Steinhagen-Thiessen, E., ... Demuth, I. (2018). Validation of a single factor representing the indicators of metabolic syndrome as a continuous measure of metabolic load and its association with health and cognitive function. *PLoS ONE, 13*(12), Article e0208231. https://doi.org/10.1371/journal.pone.0208231

Lifebrain

www.lifebrain.uio.no

BASE and BASE-II are participating in Lifebrain, a consortium of European studies funded by the EU Horizon 2020 Framework Programme. Lifebrain aims at identifying determinants of healthy lifespan development by integrating and harmonizing data and results from 11 large and predominantly longitudinal European samples from seven countries. This has yielded a database of fine-grained measures focusing on brain and cognition from more than 7,000 individual participants. A further goal of Lifebrain is to develop better statistical tools and routines for meta-analyzing longitudinal data.

Lifebrain consortium members also conducted a qualitative study to collect views and attitudes on the brain, personalized brain health, as well as interest in maintaining a healthy brain. Interviews were conducted in Spain, Norway, Germany, and the United Kingdom (Friedman et al., 2019). A global brain health survey at https://nettskjema.no was launched in 2019 to systematically explore public perceptions of personalized brain health.

Lifebrain Researchers at the MPI for Human Development

Ulman Lindenberger	Sandra Düzel
Simone Kühn	Maike M. Kleemeyer
Andreas M. Brandmaier	Ylva Köhncke

women. In men, the metabolic load factor was also related to fluid intelligence. In a study conducted with colleagues from RHYME, structural integrity of the LC integrity was found to correlate positively with individual differences in learning and memory, both across age groups and within the group of older adults (Dahl et al., 2019; for details, see pp. 128 ff.)

In another line of work, we have examined neurobiological correlates of associations between psychosocial factors and cognitive performance. In particular, we have focused on people's future time perspective (FTP). In a special issue of *GeroPsych* (Düzel & Gerstorf, 2018a), we compiled five empirical reports from different areas of psychology to showcase the multifaceted nature of FTP, delineating its antecedents, correlates, and consequences at experiential, physiological, and behavioral levels of analysis. For instance, Düzel, Drewelies et al. (2018) reported that FTP dimensions assessing cognitive and physical future lifestyles are differentially linked with brain regions known to process future planning and represent bodily states, respectively. In a study on loneliness, we found that individuals with higher self-reported loneliness tended to have smaller gray matter volumes of brain regions that are central to cognitive processing and emotional regulation, even after statistically controlling for social network size (Düzel et al., 2019). Presumably, individuals reporting higher loneliness might be less likely to engage in active, socially and cognitively stimulating lifestyles that, in turn, might contribute to brain maintenance and the preservation of cognitive abilities (Nyberg & Lindenberger, 2020). Taken together, these results suggest that psychosocial behaviors and cognitive aging are linked through multiple neurobiological mechanisms and pathways. A mechanistic and individualized understanding of these links might facilitate the design of effective strategies for preserving cognitive health in old age.

The physical environment and neighborhood characteristics are also likely contributors to individual health and well-being. Some regional characteristics such as noise and pollution affect health directly, whereas other regional characteristics might affect health and well-being indirectly by either providing resources or limiting their use. To explore such dependencies, BASE-II has linked georeferencing data to brain characteristics at the individual level. Motivated by animal models of enriched environments, we used confirmatory factor analysis to represent the structural integrity of three brain regions at the latent level and then explored associations between brain integrity and the relative amounts of forest, urban green, water, and wasteland around the home address. A positive association between amygdala integrity and forest coverage was found, pointing to its potentially salutogenic effects (Kühn, Düzel et al., 2017). This line of work will be pursued further in collaboration with the Lise Meitner Group for Environmental Neuroscience led by Simone Kühn (see pp. 185 ff.).

Future Research Directions

In the meantime, multiple waves of data have been collected in BASE-II, turning it into a veritable longitudinal data set, with currently up to 8 years of longitudinal data. We are now setting up structural equation models that quantify level and change dependencies among cognitive abilities, the integrity of various brain regions, and their interrelations. We also continue our efforts to harmonize behavioral and MR data across the various studies and sites of the Lifebrain consortium to aid cross-country comparison and generalization. An initial result of this approach is a study reporting associations between self-reported sleep and hippocampal atrophy (Fjell et al., 2020).

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Overview of the Berlin Aging Study (BASE)

www.base-berlin.mpg.de

The multidisciplinary Berlin Aging Study (BASE), initially directed by the late Paul B. Baltes and Karl Ulrich Mayer, was started in 1989. Ulman Lindenberger is the current BASE speaker. The study spans eight measurement occasions spaced over 18 years. Its distinguishing features include (1) a focus on the very old (70 to 100+ years); (2) a locally representative sample, stratified by age and sex; and (3) a broad-based interdisciplinarity (originally involving two research units from the Freie Universität Berlin, Internal Medicine and Psychiatry, and two from this Institute, Sociology and Psychology). In addition to discipline-specific topics, four integrative theoretical orientations guide the study: (1) differential aging, (2) continuity versus discontinuity of aging, (3) range and limits of plasticity and reserve capacity, and (4) aging as a systemic phenomenon.

The initial focus of BASE (1990–1993) was to obtain a heterogeneous sample, stratified by age and sex, of individuals from the western districts of Berlin aged 70 to 100+ years. A core sample of 516 men and women completed the Intensive Protocol comprising detailed measures from all four participating disciplines. Seven longitudinal follow-ups involving different depths of assessment were completed at approximately 2-yearly intervals. Details of the research design and assessment protocols can be found on the BASE website. The core sample formed the basis of the analyses reported in two monographs (see Baltes & Mayer, 1999; Lindenberger et al., 2010). Current work uses the longitudinal data to address issues such as variability and change, mortality prediction, self-related change, and genetic and socioeconomic predictors of cognitive change.

The Berlin Aging Study: International Research Group

Julia A. M. Delius	MPI for Human Development, Berlin, Germany
Alexandra M. Freund	University of Zurich, Switzerland
Denis Gerstorf	Humboldt-Universität zu Berlin, Germany
Paolo Ghisletta	University of Geneva, Switzerland
Christiane Hoppmann	University of British Columbia, Vancouver, Canada
Dana Kotter-Grühn	North Carolina State University, Raleigh, USA
Shu-Chen Li	Technische Universität Dresden, Germany
Ulman Lindenberger	MPI for Human Development, Berlin, Germany (Speaker)
Nilam Ram	Pennsylvania State University, University Park, USA
Jacqui Smith	University of Michigan, Ann Arbor, USA (Co-Speaker)
Ursula M. Staudinger	Columbia University, New York, USA
Elisabeth Steinhagen-Thiessen	Charité Universitätsmedizin Berlin, Germany
Gert G. Wagner	MPI for Human Development, Berlin, Germany (Max Planck Fellow)

Overview of the Berlin Aging Study II (BASE-II)

www.base2.mpg.de

The central objective of the multidisciplinary and multi-institutional longitudinal Berlin Aging Study II (BASE-II; see Bertram et al., 2014) is to promote a better understanding of individual differences and trajectories in cognitive, psychosocial, and physical functioning by integrating multidisciplinary perspectives and data. In doing so, it conceives of aging as a systemic phenomenon and seeks to delineate sources of heterogeneity in aging trajectories. BASE-II samples molecular genetic and immunological markers and uses instruments from the German Socio-Economic Panel (SOEP) that provide georeferencing data and information about participants' socioeconomic background and living conditions. BASE-II is structured into four research units: (1) Psychology, (2) Sociology (including Economics) and Survey Methods, (3) Medicine (including Immunology), and (4) Molecular Genetics. Like its predecessor BASE, BASE-II follows a longitudinal design: At the first wave of measurements (T1), the BASE-II sample consisted of 1,600 participants aged 60 to 80 years and 600 individuals aged 20 to 35 years. Data collection of the first wave was completed in 2014. In close collaboration with Simone Kühn, eligible BASE-II participants ($n = 445$) were additionally invited for a structural magnetic resonance imaging (MRI) assessment of the brain, comprising T1-weighted imaging, resting state data, diffusion tensor imaging, and high-resolution imaging of the hippocampus. In 2015, this MR subsample was invited again for another wave of cognitive and psychosocial assessments and a second MRI session ($n = 327$). In November 2017, the older cohort of 1,600 men and women from the original BASE-II sample was re-invited in the context of the project, Sex- and Gender-Sensitive Prevention of Cardiovascular and Metabolic Disease in Older Adults in Germany (*GendAge,* funded by the Federal Ministry of Education and Research). *GendAge* includes most of the medical and biological assessments of T1, along with a third wave of cognitive and psychosocial assessments. In addition, accelerometers are used to track participants' physical activity and sleep for a week. This data collection is ongoing and will contribute to BASE-II, allowing us to further investigate individual differences in aging trajectories (for an overview, see Demuth et al., 2019).

The Berlin Aging Study II: Steering Committee

Denis Gerstorf	Humboldt-Universität zu Berlin, Germany (Speaker)
Lars Bertram	Universität zu Lübeck, Germany
Ulman Lindenberger	MPI for Human Development, Berlin, Germany
Elisabeth Steinhagen-Thiessen	Charité Universitätsmedizin Berlin, Germany
Graham Pawelec	University of Tübingen, Germany
Gert G. Wagner	MPI for Human Development, Berlin, Germany (Max Planck Fellow)

Coordination

Ludmila Müller	MPI for Human Development, Berlin (as of 08/2019)
Katrin Schaar	MPI for Human Development, Berlin (until 07/2019))

Research Project 4: Mechanisms and Sequential Progression of Plasticity

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.

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).

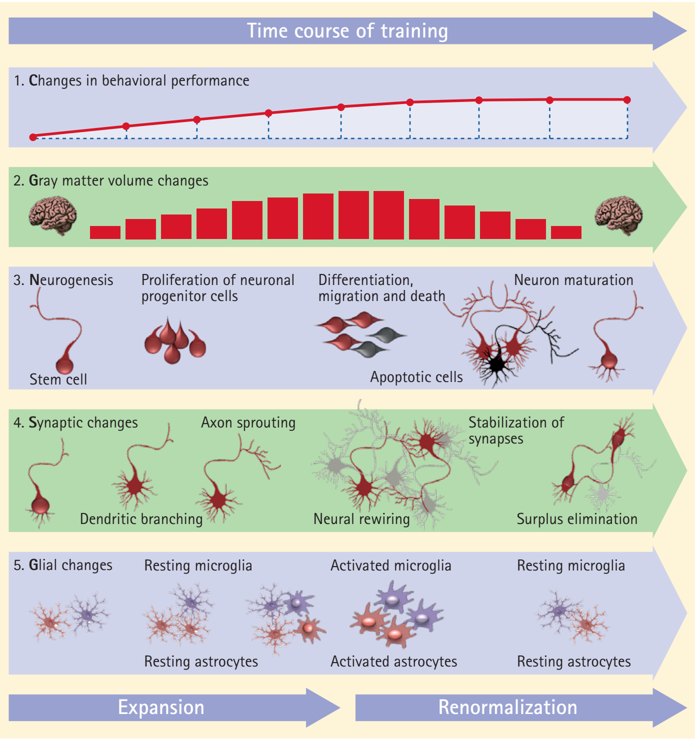

Figure 12. Schematic illustration of potential cellular changes underlying gray matter volume expansion and renormalization as detectable with magnetic resonance (MR) images (adapted from Wenger, Brozzoli et al., 2017).

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).

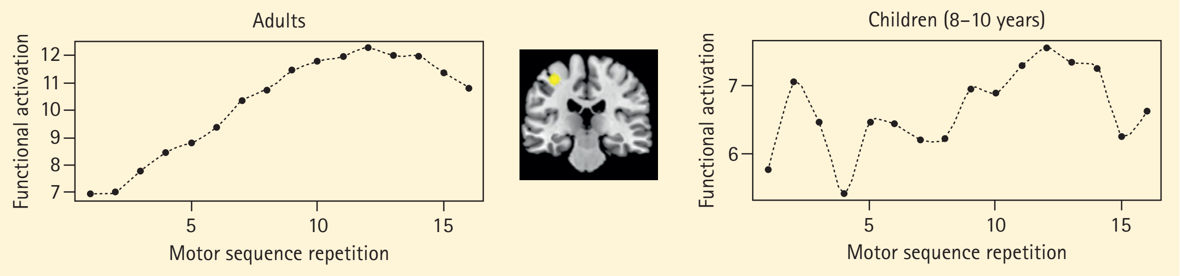

Figure 13. The learning of a novel motor sequence is associated with greater changes in left motor cortex activity in adults than in children. While adults' motor cortex activity increased with the repeated execution of the sequence and increasing proficiency, children's motor cortex was already engaged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

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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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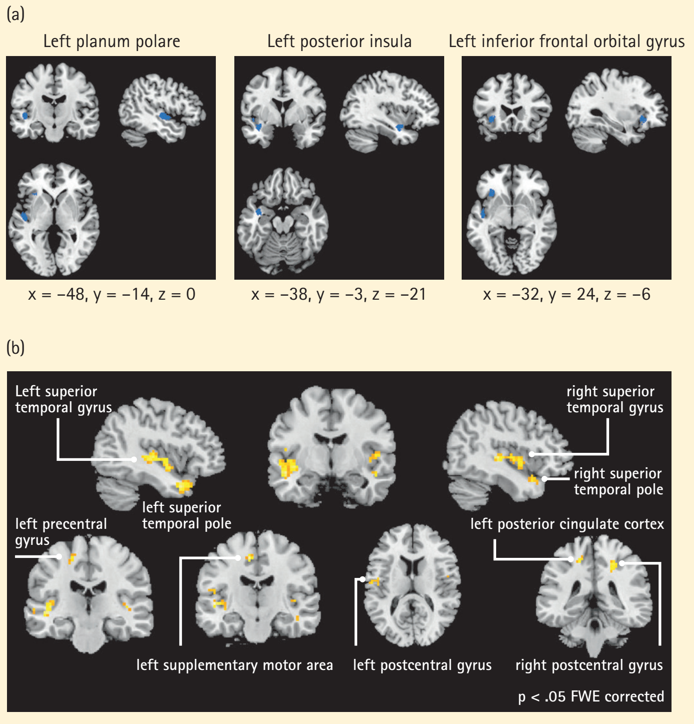

Figure 14. (a) While preparing for their entrance exam, aspiring professional musicians showed decreases in gray matter in the left planum polare, posterior insula, and left inferior frontal orbital gyrus. (b) In the aspiring professionals, but not among the amateur musicians, the biggest cluster of 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.

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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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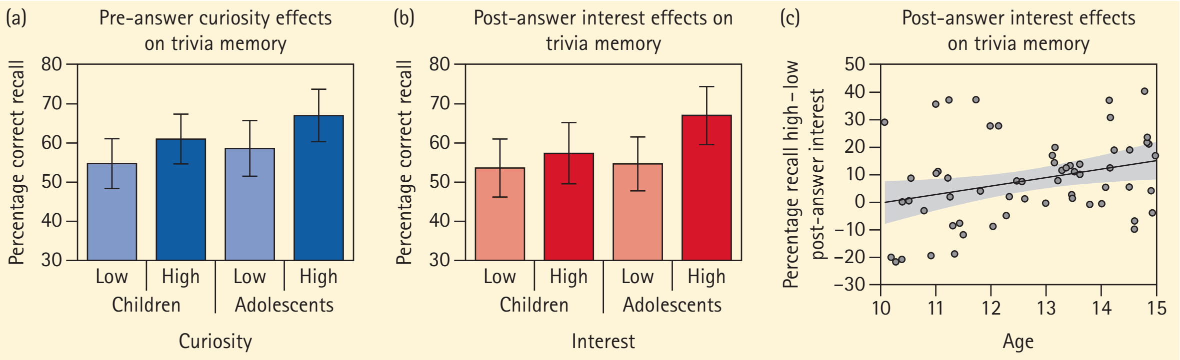

Figure 15. Children showed greater learning benefits for trivia questions that they were more curious about. In adolescents, learning was also modulated by how interesting they thought the actually presented answer was, such that they were more likely to remember the answer when initial curiosity was 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.

Research Project 5: Interactive Brains, Social Minds

Research Scientists

Viktor Müller
Ulman Lindenberger

Caroline Szymanski
(until 07/2018)

In everyday life, people often coordinate their actions. Common examples include walking with someone at a set pace, playing team sports, dancing, playing music in a duet or group, as well as a wide range of social bonding behaviors, such as gaze coordination between mother and infant or between partners. The developmental and social significance of these interpersonally coordinated behaviors is undisputed, but little, if anything, is known about the brain mechanisms that regulate their temporal dynamics. The *Interactive Brains, Social Minds* project investigates behavioral, somatic, and neural mechanisms that permit individuals to coordinate their behavior in time and space (see Figure 16).

The project has continued its major focus on analyzing electroencephalographic (EEG) data of skilled musicians playing music together. In our initial study with guitar duets, we discovered that interpersonally coordinated actions are preceded and accompanied by within-brain synchrony and between-brain oscillatory couplings (Lindenberger et al., 2009). We replicated and extended these original findings in a series of follow-up studies. In analyses of hyper-brain networks based on EEG data from a guitar quartet (Müller, Sänger et al., 2018), we found that within-brain connections tend to operate at higher frequencies (e.g., beta, gamma) than between-brain connections (e.g., delta, theta)—

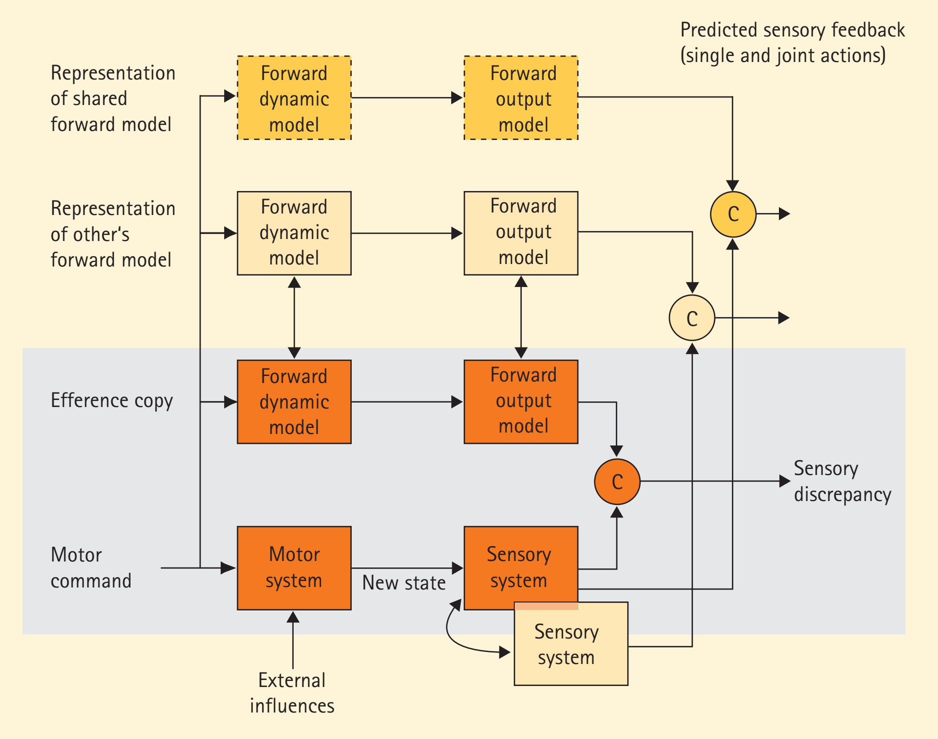

Figure 16. A forward model of interpersonal action coordination. Drawing on the work of Steven M. Boker, Wolfgang Prinz, Daniel Wolpert, and others, our model assumes that interpersonal action coordination is based on a set of linked representational layers. The single-person layer is shaded in gray. Individuals acting together attempt to synchronize their forward model regarding their own actions with their forward model regarding the other person's actions. Highly skilled individuals, such as dancers or musicians, may represent jointly performed activities as a unified suprapersonal action with a joint forward model and partially joint sensory feedbacks. The various representational layers of the actors are intertwined by sensorimotor feedback loops (see also Sänger et al., 2011).

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Sänger, J., Lindenberger, U., & **Müller, V.** (2011). Interactive brains, social minds. *Communicative & Integrative Biology, 4*(6), 655–663. https://doi.org/10.4161/cib.17934

in line with our previous results on guitar duets. Furthermore, we observed evidence for hyper-brain modules that include nodes from two, three, or even four brains (see Figure 17). We also extended our analyses to explore the dynamics of interpersonal action coordination at neural and behavioral levels of analysis during free guitar improvisation. We found that guitarists' brains were in sync with slow-frequency modulations of guitarists' acoustic signals. This provides evidence for brain–behavior entrainment reflecting temporal dynamics of coordinated music performance (Müller & Lindenberger, 2019).

We also explored the utility of hyper-frequency, hyper-brain networks in a data set of couples engaged in romantic kissing that was originally published in 2014. Oscillations in the alpha band played a central role in coordinating the two brains. Also, hyper-brain network strengths were higher and characteristic path lengths were shorter when individuals were kissing each other than when they were kissing their own hand. Between-brain strengths of theta oscillations (around 5 Hz) were reliably associated with reported partner-oriented kissing satisfaction, especially over frontal and central electrodes. Given our earlier observations of fronto-central between-brain synchronization in guitar players, we suggest that these couplings reflect cell assemblies representing movement coordination among interacting partners.

During the reporting period, we also re-analyzed the cardiac, respiratory, and vocalizing data from 11 singers and 1 conductor engaged in choir singing, originally published in 2011. We showed in greater detail how cardiac, respiratory, and voice production subsystems interact among each other both within and across singers as a function of whether a canon is sung in unison or in different voices. Notably, we found that the conductor's hand movements are synchronized with each of the three subsystems (Müller et al., 2018). With regard to network topology, we found that clustering coefficients as well as local and global efficiency were highest and characteristic path lengths, correspondingly, shortest when the choir sang a canon in parts as compared to singing it in unison. Furthermore, network metrics revealed a significant relationship to individuals' heart rate, presumably indicating arousal, and to an index of heart rate variability, reflecting the balance between sympathetic and parasympathetic activity. Based on this work, we propose that network topology dynamics capture essential aspects of group behavior and may represent a potent biomarker of social interaction dynamics (Müller et al., 2019).

In a related line of work, the project has sought to devise new EEG paradigms that are suited to observe the behavioral functions of inter-brain synchrony under experimentally more controlled conditions (Dissertation Caroline Szymanski). In one of these studies (Szymanski, Pesquita et al., 2017), participants were asked to perform a visual search task either alone or with a partner. Local phase synchronization and between-brain phase synchronization were generally higher when partners attended to a visual search task jointly than when they attended to the same task individually. Also, between-team differences in behavioral performance gain during the joint condition were associated with between-team differences in local and inter-brain phase synchronization. These results suggest that phase synchronization is a neural correlate of social facilitation that might help to explain why some teams perform better than others. A second study has tested whether same-frequency, same-phase transcranical alternating-current stimulation (tACS) is associated with greater behavioral synchrony in a dyadic drumming task than no stimulation or stimulation that differs in phase and frequency. Contrary to expectations, both stimulation conditions were associated with greater dyadic drumming *asynchrony* relative to the sham (no stimulation) condition. No influence of hyper-tACS on behavioral performance was seen when participants were asked to drum separately in synchrony to a metronome (Szymanski, Müller et al., 2017). These results indicate that the interactions between externally triggered and intrinsically generated frequencies and phases require further theoretical and empirical work.

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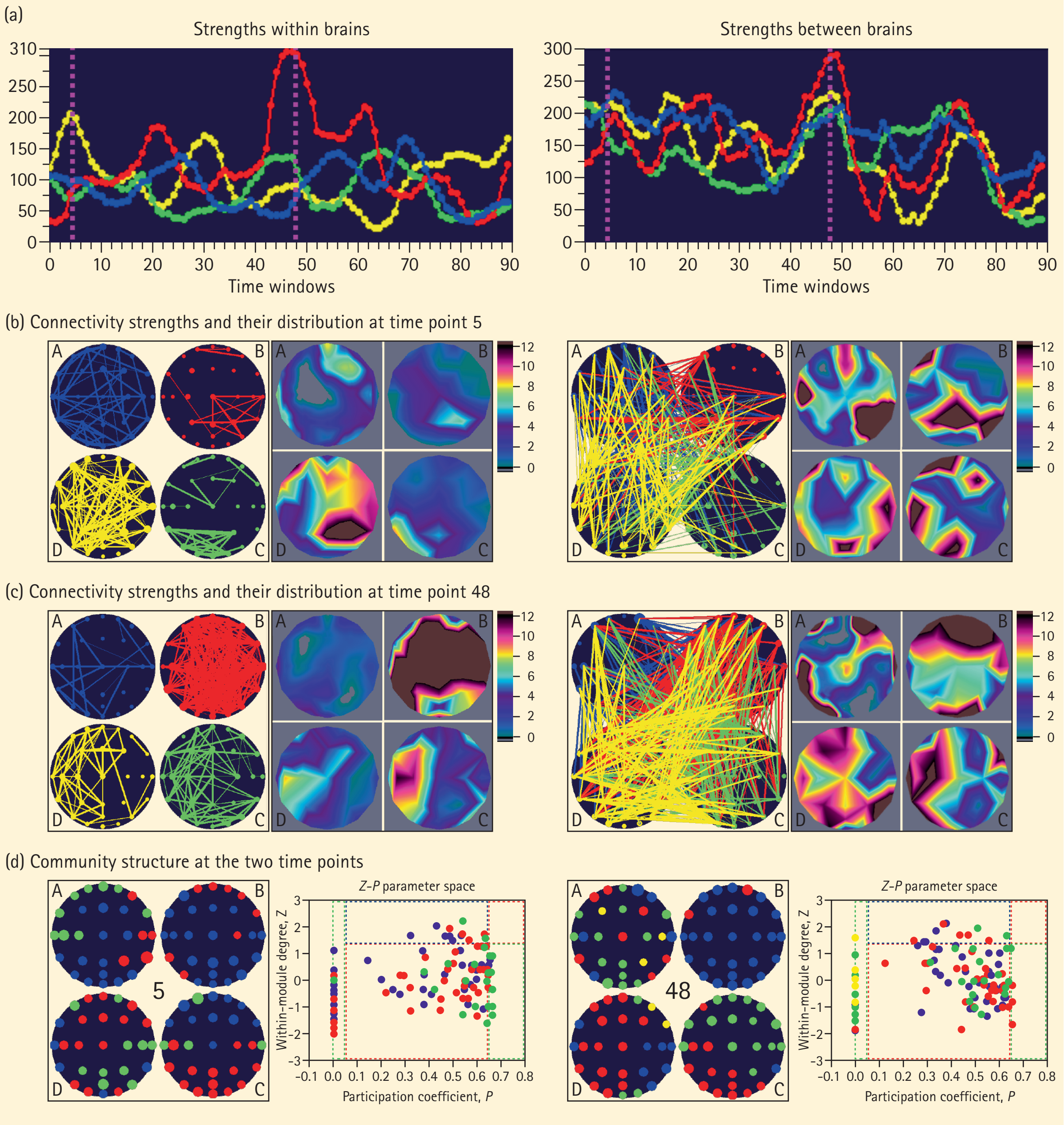

Figure 17. Coupling strengths and connectivity brain maps while playing guitar in a quartet, assessed in a moving window approach. (a) Time course of within- and between-brain out-strengths in the four guitarists. (b) Brain connectivity maps and distribution of strengths within (left panel) and between (right panel) the brains at time window 5. (c) Brain connectivity maps and distribution of strengths within (left panel) and between (right panel) the brains at time window 48. Note that the colors in (a) to (c) correspond to the different guitarists. The time windows are indicated by dotted vertical lines in (a). Strong within- and between-brain connectivity is evident in the first time window (5), when guitarist D (shown in yellow) is playing alone. In the second time window (48), when the musical theme begins to be repeated, strong within- and between-brain connectivity is evident in guitarist B (shown in red). (e) Modularity or community structures of hyper-brain networks with *Z-P* parameter space across the same time windows. Modules are coded by color. Note that most modules share nodes across two, three, or even four brains (adapted from Müller, Sänger, & Lindenberger, 2018).

Research Project 6: Brain Imaging Methods in Lifespan Psychology

Research on human development seeks to delineate the variable and invariant properties of age-graded changes in the organization of brain–behavior–environment systems. In this vein, various magnetic resonance imaging (MRI) modalities, including magnetic resonance spectroscopy (MRS), have become indispensable, as they allow for the noninvasive assessment of brain function, anatomy, microstructure, and metabolism.

The two main goals of the *Brain Imaging Methods* project are to: (a) ascertain and improve the measurement quality of standard brain imaging protocols at the Center; and (b) complement the standard imaging repertoire by advanced sequences with enhanced interpretability that hold promise in elucidating structural changes and physiological mechanisms related to maturation, learning, and senescence. In pursuing these goals, the project serves as a resource to other projects interested in imaging (e.g., Bender et al., 2018; Dahl et al., 2019; Keresztes et al., 2017; Kleemeyer et al., 2017; see Figure 18).

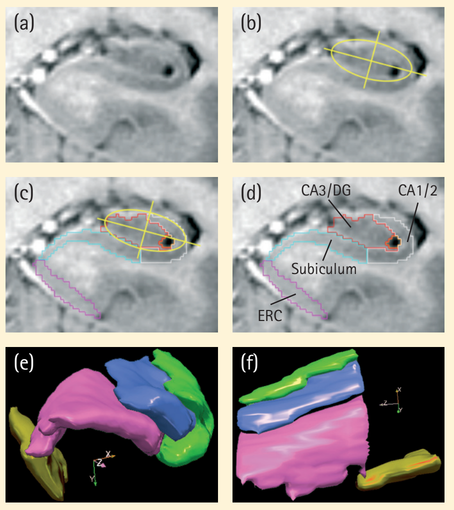

Figure 18. Illustration of the anatomic-geometric heuristic for manual morphometry. (a) A representative slice of anterior hippocampal (HC) body following the visualization of the uncal sulcus. To facilitate tracing, the T_2-weighted contrast has been inverted to mimic a T_1-weighted image. (b) Placement of the ellipse and bisecting lines (the major and minor axes of the ellipse). (c) The minor axis bisecting the ellipse marks the point from which a vertical line is dropped to create a boundary separating the subiculum from CA1/2, and CA 1/2 from CA3–4/DG, as shown in (d). Bottom: 3-D illustrations of sagittal (e) and oblique coronal (f) views of manual subfield labeling in the HC body from one participant (adapted from Bender et al., 2018).

Structural and quantitative MRI methods occupy a central place in the project. During the reporting period, the project has focused on: (a) T_1-mapping by means of an MP2RAGE acquisition protocol to obtain estimates of laminar myelination across the cortical sheet; (b) myelin water fraction (MWF) imaging, which maps the fraction of short T_2 relaxation rates quantitatively and appears to yield more valid estimates of myelin than other widely used methods; (c) advanced methods in high angular resolved diffusion imaging (HARDI), from which maps of water diffusion in brain tissue can be deduced that permit estimates of local axonal orientation and thereby enable the identification of particular fiber tracts in white matter; and (d) neuromelanin-sensitive high-resolution imaging of the brainstem to determine the individual position and extent of the loci coerulei (Dahl et al., 2019). *Functional MRI and MRS* are used to provide maps and spectra of brain activity during task performance or at rest. The project takes special interest in: (a) functional imaging with high spatial or temporal resolution by exploiting multiband echo-planar imaging (MB-EPI) acquisition strategies; and (b) task-related, time-resolved applications of proton MRS, with a focus on glutamate. Work on MR spectroscopy and MWF imaging, on the one hand, and on T_1 mapping, on the other, has been done in collaboration with Jeffrey A. Stanley (Wayne State University, Detroit, USA) and José P. Marques (Donders Institute, Radboud University, Nijmegen, Netherlands), respectively. For more information about the Institute's MRI facility, see p. 298.

T_1 Mapping Using MP2RAGE With B_1 Map Corrections

The longitudinal relaxation time T_1 in the cortex is affected by the myelin content in the laminae. T_1 mapping offers a noninva-

Research Scientists

Nils C. Bodammer

Ulman Lindenberger
Naftali Raz
Davide Santoro

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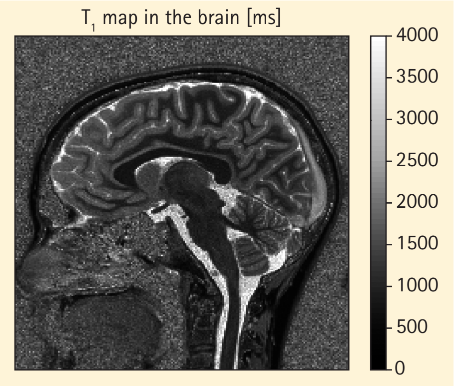

Figure 19. Typical T_1 map of a child's brain (1 slice out of a 3D volume) obtained with our protocol using MP2RAGE and B_1 map correction.

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sive method to determine cortical structures and their changes over time. We have been developing a new protocol that makes use of multiple MP2RAGE sequences developed by José Marques and colleagues for the accurate estimation of high-resolution T_1 maps in the full brain. We have chosen tailored paired values for the inversion times to cover the whole range of T_1 values in the brain. The resulting T_1 map is then corrected by a B_1 map to cancel hardware imperfections and radio frequency inhomogeneities across the brain (see Figure 19). The B_1 mapping method used (Santoro et al., 2011) was optimized in-house for our studies. The full protocol for a 1 mm isotropic T_1 map of the full brain of children takes about 16 minutes, with work in progress to reduce its duration.

Myelin-Water Fraction Imaging (MWF)

Based on a time series of T_2-weighted MR images with increasing echo-times acquired by a 3D GRAdient and Spin-Echo (GRASE) sequence, MWF imaging evaluates the transversal relaxation in a multiexponential manner by applying a nonnegative least squares (NNLS) fitting algorithm. The fraction of short T_2s (< 40 ms) provides an estimate of the portion of water molecules located between myelin sheaths, presumably reflecting the degree of myelination within white matter (Arshad et al., 2017).

High Angular Resolved Diffusion Imaging (HARDI)

Diffusion imaging captures the movement of water molecules, termed diffusion. Diffusion in tissue is hindered by cell membranes. Therefore, the orientation-dependent diffusion profiles provide information about tissue microstructure. For instance, when water molecules are observed in myelinated neuronal fibers, their diffusion is hampered less along than across fiber tracts. Hence, principal diffusion directions can be identified with the orientations of axonal tracts. Special MR protocols sensitized to the diffusion of water molecules in tissue allow to measure such diffusion orientation profiles. In his thesis, Maximilian M. Wichmann (2018), a master's student in our project, determined the precision and estimates of accuracy of the analyzed principal diffusion directions as a function of the diffusion-sensitizing gradient scheme and the model to describe diffusion profiles. The tensor model was significantly outperformed by two competing models (sticks-and-ball, constrained spherical deconvolution).

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Research Project 7: Formal Methods in Lifespan Psychology

Since its foundation by the late Paul B. Baltes in 1981, the Center for Lifespan Psychology has sought to promote conceptual and methodological innovation within developmental psychology and in interdisciplinary context. Over the years, the critical examination of relations among theory, method, and data has evolved into a distinct feature of the Center. The overarching objective of the *Formal Methods* project is to test theories, develop methods, and explore research designs that articulate human development across different timescales, levels of analysis, and functional domains. The temporal resolution of data relevant for lifespan research varies widely, from the millisecond range provided by behavioral and electrophysiological observations to the small number of occasions spread out across several years provided by longitudinal panel studies. The project is based on the premise that a comprehensive understanding of human development across the lifespan requires a person-oriented, multivariate, and longitudinal approach. Such high-density, large data sets offer great opportunities for discovery and hypothesis testing, but also pose new theoretical and methodological challenges. The project meets these challenges by a strong emphasis on *methodology,* understood as the reciprocal interplay between concepts and methods that is at the heart of scientific progress.

In line with its interest in delineating and explicating individual differences in change, the project has continued and expanded its work on Structural Equation Modeling (SEM) and hierarchical state-space methods, both of which integrate a wide range of different multivariate analysis techniques. During the reporting period, project members have shown how these approaches can assist researchers in: (a) optimally planning longitudinal studies under constrained resources; (b) refining or modifying hypotheses through comprehensive exploratory data analysis; (c) appropriately modeling unequally spaced measurements, context effects, and individual differences in longitudinal research; and (d) modeling the dimensionality of age-related changes in cognition.

New Methods for Analyzing Change

Longitudinal panel studies are a key empirical method to chart between-person differences in behavioral and neural development. The project members have been working on developing and evaluating new methods to analyze change. Most dynamic models (e.g., cross-lagged panel models) currently in use in psychological research assume that measurement occasions are equally spaced in time. This failure to account for unequal spacing of measurement occasions may seriously bias parameter estimates. Driver, Oud, and Voelkle (2017) have developed a software package for the estimation of hierarchical continuous-time system dynamics, called *ctsem* (continous-time structural equation modeling). The package is suited for the analysis of panel data (repeated observations from more than one individual) and time-series data (repeated observations from one individual). Using stochastic differential equations coupled with a measurement model, *ctsem* accommodates any pattern of measurement occasions. *ctsem* can estimate relationships over time for multiple latent processes, measured by multiple noisy indicators with varying time intervals between observations (see Figure 20). With recent developments in hierarchical and nonlinear modeling, as well as Bayesian estimation (Driver & Voelkle, 2018a), parameters themselves can be modeled as slowly changing dynamic states. Coupled with the inclusion of event- and intervention-related effects over time (Driver & Voelkle, 2018b), this allows for the high level of model expressiveness that is necessary for developing and testing theories of development across multiple timescales.

Andreas Brandmaier and Timo von Oertzen have continued their work on Ωnyx, a freely available software environment for creating and estimating SEM. The software offers a graphical user interface to facilitate the specification of models and includes a powerful back-end for performing parameter estimation (von Oertzen et al., 2015).

Research Scientists

Andreas M. Brandmaier

Janne Adolf
(until 10/2017)
Marie K. Deserno
(as of 12/2019)
Charles C. Driver
Nina Karalija
(09/2018–02/2019)
Maike M. Kleemeyer
(as of 09/2019)
Ylva Köhncke
(as of 07/2017)
Ulman Lindenberger

Manuel Arnold
(COMP2PSYCH;
as of 10/2017)

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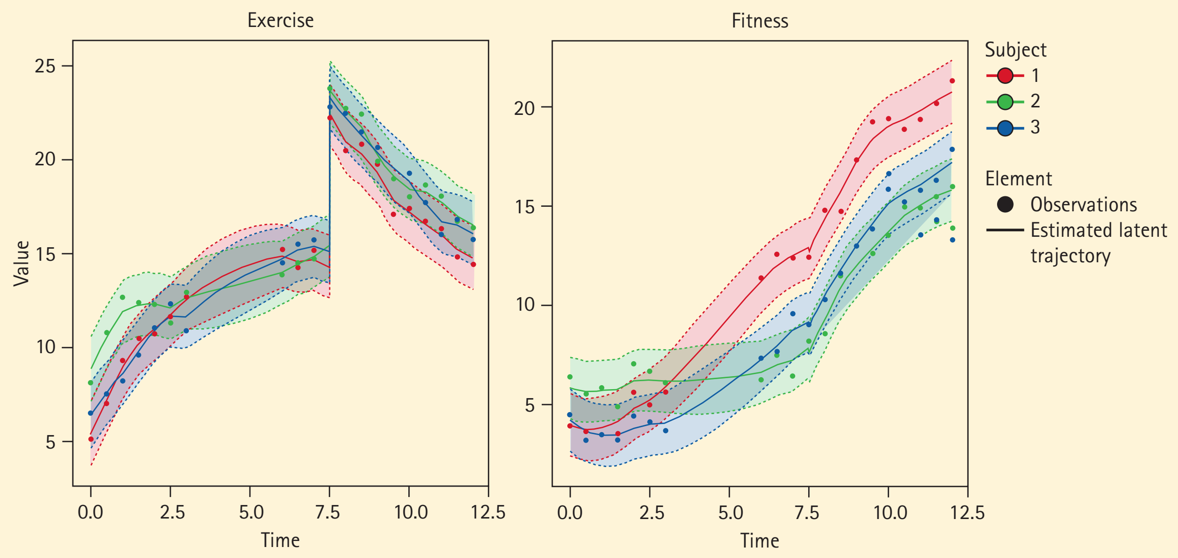

Figure 20. Estimated latent processes from a simulated hierarchical dynamic system of fitness and exercise. After a motivation intervention temporarily increasing exercise levels, fitness rises more quickly until exercise drops back to an equilibrium level determined by specific characteristics of the subject.

Optimizing the Design of Longitudinal Studies

Longitudinal studies often require a large investment of resources. In earlier work, we have shown how design-related choices, such as the number of individuals or number of measurement occasions, affect statistical power and how optimal choices maximize the efficiency of longitudinal designs while keeping power constant (Brandmaier et al., 2015). In the meantime, we have extended this framework to arrive at an integrated understanding of measures of precision, reliability, and effect size for individual differences in change (Brandmaier, von Oertzen et al., 2018). Thus far, cognitive neuroscience has paid relatively little attention to questions of reliability and statistical power. For instance, surprisingly little is known about the psychometric properties of measures attained from structural and functional magnetic resonance imaging (fMRI) protocols. We have introduced the intraclass effect decomposition (ICED) framework to overcome this shortcoming (Brandmaier, Wenger et al., 2018). With ICED, researchers can separate and quantify the effects of different measurement characteristics, such as day, session, or scanner, on measurement reliability. Using this framework, we showed that some standard designs, such as 5 minutes of resting-state functional connectivity assessment, come with low reliability that hardly affords any kind of statistical inference about individual differences. We hope that ICED will encourage and assist researchers in delineating sources of unreliability and guide them in developing more efficient research designs.

To increase statistical power or achieve identical power with fewer measurements, planned missingness (PM) is a convenient but often overlooked design option. In PM designs, participants are tested on a random subset of all possible measurement occasions, thereby reducing potential resource bottlenecks, such as those arising from limited availability of an MR scanner, as well as research participants' testing load. To find optimal PM designs, we developed an asymptotic approach to generate, evaluate, and select optimal longitudinal designs for measuring change with PM (Brandmaier et al., 2020).

In research on adult cognitive development, available theories of change often posit nonlinear (e.g., exponential) decline. However, growth models used for data analysis typically

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Exploration and Model Testing

Building models fully informed by theory is impossible when data sets are large and theoretical predictions are not available for all variables and their interrelations. In such instances, researchers may start with a core model guided by theory and then face the problem of which additional variables should be included. In earlier work, we have shown that SEM Trees and Forests provide a straightforward solution to this variable selection problem (Brandmaier et al., 2016). SEM Trees hierarchically split empirical data into homogeneous groups sharing similar parameters of a model by recursively selecting optimal predictors from a potentially large set of candidate predictors. SEM Forests aggregate predictive information over a set of trees

Coupled Cognitive Changes in Adulthood

With advancing adult age, cognitive abilities such as memory, processing speed, and reasoning tend to decrease. At the same time, there are marked individual differences in rates of change, with some adults showing maintenance and select improvements and others showing precipitous decline. To shed light on the dimensionality of cognitive aging, we revisited a classical question posed by Patrick Rabbitt more than 25 years ago: "Does it all go together when it goes?" Specifically, we conducted a meta-analysis to examine the degree to which changes in different cognitive abilities in adulthood and old age are correlated (Tucker-Drob et al., 2019). Across 22 unique data sets with over 30,000 individuals, a common factor of change accounted for 60% of the reliable variance in cognitive change (see Figure 21). The couplings among rates of changes increased with advancing adult age, presumably reflecting "dynamic dedifferentiation" or the increasing importance of an ensemble of common causes on cognitive change. Notably, abilities showing little average decline, such as verbal knowledge, contributed to common change to about the same extent as abilities showing pronounced average decline, such as perceptual speed. Hence, individuals who improve more on verbal knowledge relative to others are likely to decline less in perceptual speed. This generalized pattern of change adds to an important qualification to two-component theories of intellectual development in adulthood, such as the Cattell/Horn theory of fluid versus crystallized intelligence.

Box 1.

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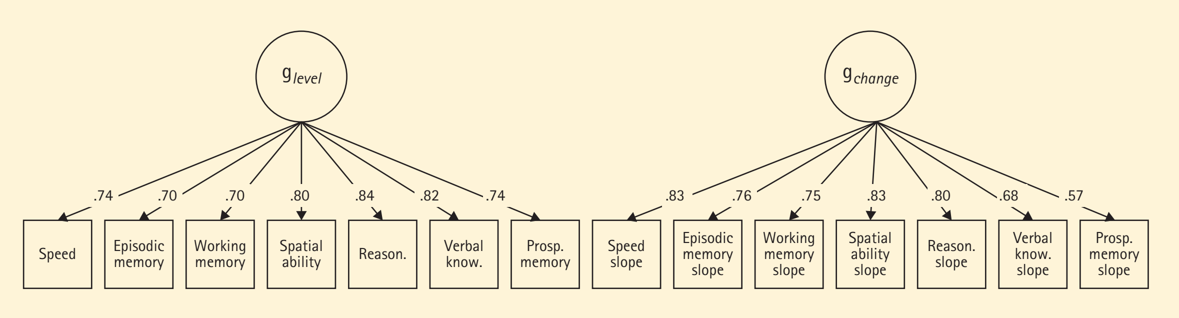

Figure 21. Path diagram representing meta-analytic estimates for standardized factor loadings of individual cognitive abilities on a general factor of levels (left) and standardized factors loadings of longitudinal slopes for individual cognitive abilities on a general factor of changes (right). Variances were omitted from the diagram. Reason. = Reasoning; Verbal know. = Verbal knowledge; Prosp. memory = Prospective memory (adapted from Tucker-Drob et al., 2019).

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and yield a measure of variable importance that is more robust than corresponding measures from single trees. Variable importance guides researchers on what variables may be missing from their models and the underlying theories. In a recent application of SEM Forests, we investigated longitudinal trajectories of well-being toward the end of life using data from the German Socio-Economic Panel study. We found that individual differences in the decline of well-being are associated with factors related to physical health, social participation, and perceived control (Brandmaier et al., 2017).

Longitudinal data sets with dense observations generally offer great opportunities for discovery and hypothesis testing. Therefore, we have merged the *ctsem* approach described above with SEM Trees into CTSEM Trees (Brandmaier et al., 2018). When the goal is variable selection to build predictive models with linear effects only, we introduced a further method, regularized SEM, that brings the idea of regularization to SEM and allows one to build simple models from high-dimensional data while optimizing predictive accuracy (Jacobucci et al., 2019).

Ongoing work in this area extends the model of interest from SEM to any statistical model and seeks to quantify the mismatch between the specified model and the "best possible" model using information theoretic approaches. Inferences drawn from models are generally contingent on the models being "correct," at least in certain ways. However, checking this premise often occurs ad-hoc based on a variety of misspecification indices. Levels of mismatch between model and data that derived from information theory might guide model refinement more efficiently than currently available approaches.

Between-Person Differences and Within-Person Changes in Cognition

Over a century of research on between-person differences in cognitive performance has resulted in the consensus that human cognitive abilities are hierarchically organized, with a general factor, termed general intelligence or "g," uppermost. Surprisingly, it is unknown whether this body of evidence, which reflects between-person differences, is informative about how cognition is structured within individuals. It is likely that many factors contributing to differences between individuals vary less, or differently, within individuals. For instance, allelic variations of the genome contribute to differences between but not within individuals. To overcome this lacuna, Schmiedek et al. (in press) analyzed data from 101 young adults performing nine cognitive tasks on 100 days distributed over six months (see Box 2). The structures of individuals' cognitive abilities were found to deviate greatly from the modal between-person structure, and to vary among each other. The g factor was much less prominent within than between persons. Working memory contributed the largest share of common variance to both between- and within-person structures. The results show that between-person structures of cognitive abilities cannot serve as a surrogate for within-person structures. To reveal the development and organization of human intelligence, individuals need to be studied over time.

Overview of the COGITO Study **www.mpib-berlin.mpg.de/cogito**

In the COGITO study, 101 younger adults (20–31 years of age) and 103 older adults (65–80 years of age) participated in 100 daily sessions in which they worked on cognitive tasks measuring perceptual speed, episodic memory, and working memory, as well as various self-report measures (see Schmiedek et al., 2010, 2020).

All participants completed pretests and posttests with baseline measures of cognitive abilities and transfer tasks for the practiced abilities. Brain-related measures were taken from subsamples of the group, including structural magnetic resonance imaging (MRI), functional MRI, and electroencephalographic (EEG) recordings.

A central goal of the COGITO study was the comparison of between-person and within-person structures of cognitive abilities. Further, the COGITO study qualifies as a cognitive training study of unusually high dosage and long duration because of its 100 sessions of challenging cognitive tasks.

Box 2.

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