Center for Lifespan Psychology

Director: Ulman Lindenberger
Research Team 2014–2016

Nils C. Bodammer, Andreas M. Brandmaier, Julia A. M. Delius, Sandra Düzel, Yana Fandakova, Douglas D. Garrett, Imke Kruse, Simone Kühn (as of 02/2017: University Medical Center Hamburg-Eppendorf, Germany), Ulman Lindenberger, Viktor Müller, Naftali Raz, Myriam C. Sander, Katrin Schaar (as of 01/2016: Humboldt-Universität zu Berlin, Germany), Sabine Schaefer (04/2015–03/2016: Leipzig University, Germany; as of 04/2016: Saarland University, Germany), Yee Lee Shing (as of 08/2015: University of Stirling, UK), Julius Verrel, Manuel C. Voelkle (as of 02/2015: Humboldt-Universität zu Berlin, Germany), Markus Weichenberger (as of 01/2015: Humboldt-Universität zu Berlin, Germany), Gert G. Wagner (Max Planck Fellow), Elisabeth Wenger, Markus Werkle-Bergner

Postdoctoral Fellows
Cathleen Bache (until 07/2016), Andrew R. Bender, Julia C. Binder, Timothy R. Brick (as of 09/2014: The Pennsylvania State University, USA), Garvin Brod (as of 05/2016: German Institute for International Educational Research [DIPF], Frankfurt a.M., Germany), Whitney G. Cole, Elisa Filevich (as of 09/2015: Leipzig University, Germany), Thomas H. Grandy (as of 03/2016: Vivantes Klinikum Am Urban, Berlin, Germany), Julian D. Karch, Attila Keresztes, Niels A. Kloosterman, Tian Liu (until 03/2015), Johan Mårtensson (as of 02/2014: Lund University, Sweden), Dionysios Perdikis (as of 05/2014: Aix Marseille University, France), John J. Prindle (as of 09/2015: University of Southern California, Los Angeles, USA), Davide Santoro, Julia Schröder, Iris Wiegand

Predoctoral Fellows
Janne Adolf (LIFE), Oisin Butler (LIFE), Martin J. Dahl (LIFE), Charles C. Driver (LIFE), Maike M. Kleemeyer (LIFE), Neda Khorasvani (LIFE), Julian Q. Kosciessa (COMP2PSYCH), Nina Lisofsky (LIFE; as of 06/2016: Agaplesion Diakonieklinikum Rotenburg, Germany), Beate E. Mühlroth (MaxNetAging Research School), Laurel Raffington, Verena R. Sommer (LIFE), Caroline Szymbanski (Berlin School of Mind & Brain)

Adjunct Researchers
Annette Brose (Humboldt-Universität zu Berlin, Germany), Simone Kühn (University Medical Center Hamburg-Eppendorf, Germany), Shu-Chen Li (Technische Universität Dresden, Germany), Martin Lövdén (Karolinska Institutet, Stockholm, Sweden), Florian Schmiedek (German Institute for International Educational Research [DIPF], Frankfurt a.M., Germany), Yee Lee Shing (University of Stirling, UK), Manuel C. Voelkle (Humboldt-Universität zu Berlin, Germany), Timo von Oertzen (as of 01/2016: Universität der Bundeswehr München, Germany)

Visiting Researchers
Randy Bautista (University of Southern California, Los Angeles, USA), Steven M. Boker (University of Virginia, Charlottesville, USA), Timothy R. Brick (The Pennsylvania State University, USA), Silvia Bunge (University of California, Berkeley, USA), Lorenza Colzato (Leiden University, Netherlands), Christopher Hertzog (Georgia Institute of Technology, Atlanta, USA), Bernhard Hommel (Leiden University, Netherlands), Mara Mather (University of Southern California, Los Angeles, USA), Ulrich Mayr (University of Oregon, Eugene, USA), Ann Pearman (Georgia Institute of Technology, Atlanta, USA), Thad Polk (University of Michigan, Ann Arbor, USA)
Introductory Overview

Founded in 1981 by Paul B. Baltes (1939–2006; Lindenberger, Delius, & Staudinger, 2015), 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 neuroscience. Work at the Center is guided by three propositions: (1) to study lifespan changes in behavior as interactions among maturation, learning, and senescence; (2) to develop theories and methods that integrate empirical evidence across domains of functioning, timescales, as well as behavioral and neural levels of analysis; (3) to identify mechanisms of development by exploring age-graded differences in plasticity. 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 continuously extended its research on behavioral development to earlier periods of life.

Three Guiding Propositions

The Center’s research agenda can be summarized by three interrelated theoretical propositions (Kühn & Lindenberger, 2016; Lindenberger, 2014; Lövdén, Bäckman, Lindenberger, Schaefer, & Schmiedek, 2010). 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 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 developing individuals. Hence, as John Nesselroade, Peter Molenaar, and others have emphasized, individual people, rather than groups of people or domains of functioning within persons, form the privileged system of analysis and explanation.

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.

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. Note, however, that maturation cannot take place without learning and that learning cannot take place without maturation. Similarly, the ways in which senescence takes its toll on the brains of aging individuals depend on their past and present learning and maturational histories. To complicate matters even more, 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. 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.

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). In contrast, other forms of neural and behavioral moment-to-moment variability may indicate an individual’s ability to bring a wide variety

Figure 2. Example for predictions linking moment-to-moment variability to long-term change and brain changes to behavioral changes. Senescent changes in neuromodulation lead to greater moment-to-moment fluctuations in neural signaling, enhance the prominence of background noise, reduce the distinctiveness of processing pathways and representations, and increase variability of cognitive performance. Aging individuals with greater moment-to-moment process fluctuations 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).

© MPI for Human Development
of different strategies to the task and are positively related to long-term change in both childhood and old age (e.g., Hertzog, Lövdén, Lindenberger, & Schmiedek, in press). To articulate these perspectives, we need to gather multivariate time-series data that capture short-term variability and long-term changes in across-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 offers more than one implementation of an adaptive behavioral outcome. 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) cultural–social as well as physical regularities of the environment.

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 (Freund et al., 2013, 2015; Kühn & Lindenberger, 2016; Lindenberger, 2014). Scientifically, inquiries into the plasticity of brain and behavior are a rich source 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 (Lövdén et al., 2010).

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). The resulting

![Figure 3](image-url)

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).
knowledge about the plasticity of developmental trajectories is essential for improving human welfare. Hence, investigations of age changes in the plasticity of development carry the potential to explain and ameliorate the expression of human potential.

For all of these reasons, age-comparative intervention studies with a focus on behavioral and neural manifestations of plasticity form the core component of empirical research at the Center. At the conceptual level, researchers at the Center have aimed at identifying distinct features of plasticity in relation to other types of behavioral and neural variability and change (Lövdén et al., 2010; see Figure 4). At the empirical level, the Center has carried out pioneering studies on plastic changes in brain and behavior, such as the COGITO study (see Intra-Person Dynamics project, pp. 157–159). In recent years, we have launched a new generation of experiments that combine behavioral skill training with repeated functional and structural imaging to directly observe the temporal progression of plasticity in individual people. Going beyond the canonical pretest–posttest design of intervention studies, these studies seek to observe how plastic changes unfold over time. In this context, Lövdén, Wenger, Mårtensson, Lindenberger, and Bäckman (2013) have noted that neural manifestations of plasticity are often marked by initial tissue expansion (e.g., overproduction of new synaptic connections) followed by renormalization (e.g., pruning of these connections). Recently, we have been able to delineate this pattern empirically in human adults (Wenger et al., 2017; see Plasticity project, pp. 153–156; see also Lindenberger, Wenger, & Lövdén, 2017).

Methodological Innovation

Since its foundation in 1981, the Center has sought to promote conceptual and methodological innovation within developmental psychology and in interdisciplinary context. Special attention is paid to methods and research designs apt to integrate (a) multiple domains of functioning, (b) multiple timescales, and (c) multiple levels of analysis. Random coefficient modeling, latent growth

---

**Figure 4.** Schematic model of a mismatch between functional supply and experienced environmental demands caused by primary changes in demand (e.g., altered experience through cognitive training). Functional supply (i.e., the structural constraints imposed by the brain on function and performance) allows for a range of performance and functioning. Flexibility denotes the capacity to optimize the brain’s performance within the limits of the current state of functional supply. Due to the sluggishness of plasticity, structural supply optimizes its support for function to a level of demand (i.e., use of functional supply) that is averaged over some unknown time period. Mismatches need to be prolonged to overcome the inertia and sluggishness of plasticity and to push the system away from its dynamic equilibrium. Deviations in demand that are within the current range of functional supply induce the mismatch that constitutes the impetus for plastic change (adapted from Lövdén, Bäckman, Lindenberger, Schaefer, & Schmiedek, 2010).

© MPI for Human Development

---

**Key References**


curve modeling, and related statistical techniques have served as versatile tools for the analysis of multivariate data with nested time structures, such as trials, blocks of trials, days, weeks, and years. Recently, time-delay embedding and clustering methods for time-series data, continuous-time structural equation modeling, combinations of classifier and structural equation modeling techniques, as well as machine-learning tools have been added to the repertoire (see Formal Methods project, pp. 172–174). Under the leadership of Gerd Kempermann from the Dresden site of the German Center for Neurodegenerative Diseases, and in collaboration with Antonio Krüger from Saarland University, Andreas M. Brandmaier and Ulman Lindenberger have continued their collaboration on an animal model of epigenetic contributions to individual development (Freund et al., 2013, 2015). Finally, the Center closely collaborates with the Max Planck UCL Centre for Computational Psychiatry and Ageing Research (see pp. 195–200).

Research Awards (Selection)
During the reporting period, several research awards were bestowed upon visitors and members of the Center. Andreas M. Brandmaier received the Heinz-Billing-Award

<table>
<thead>
<tr>
<th>Name of project</th>
<th>Researchers, including postdoctoral fellows</th>
<th>Predoctoral research fellows</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lifespan Neural Dynamics Group within the Max Planck UCL Centre</td>
<td>Douglas D. Garrett**, Niels A. Kloosterman*, Iris Wiegand*</td>
<td>Julian Q. Kosciessa</td>
</tr>
<tr>
<td>Mechanisms and Sequential Progression of Plasticity</td>
<td>Yana Fandakova**, Elisabeth Wenger**, Simone Kühn*, Ulman Lindenberger</td>
<td>Oisin Butler, Neda Khosravani</td>
</tr>
<tr>
<td>Intra-Person Dynamics Across the Lifespan</td>
<td>Manuel C. Voelkle***, Annette Brose*, Ulman Lindenberger, Florian Schmiedek*</td>
<td>Janne Adolf, Charles C. Driver</td>
</tr>
<tr>
<td>Interactive Brains, Social Minds</td>
<td>Viktor Müller**, Ulman Lindenberger</td>
<td>Caroline Szymanski</td>
</tr>
<tr>
<td>Sensorimotor–Cognitive Couplings</td>
<td>Julius Verrel**, Whitney G. Cole*, Ulman Lindenberger</td>
<td>Maike M. Kleemeyer</td>
</tr>
<tr>
<td>Brain Imaging Methods in Lifespan Psychology</td>
<td>Nils C. Bodammer**, Ulman Lindenberger, Naftali Raz, Davide Santoro*</td>
<td></td>
</tr>
</tbody>
</table>

Note. Research manager of the Center: Imke Kruse. The table refers to projects and project members as of 03/2017; for updates, visit www.mpib-berlin.mpg.de.

**principal investigator; *postdoctoral fellow; °adjunct researcher (primary affiliation with another institution).

1 Myriam C. Sander leads a Minerva Research Group (see Box 2, p. 152).

2 Gert G. Wagner is Max Planck Fellow at the MPI for Human Development (see pp. 263–268 for more information).
Overview of Research Projects at the Center for Lifespan Psychology

Currently, in March 2017, empirical and conceptual work at the Center is structured into eight research projects (see Table 1). The activities pursued in these 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 experimentally disentangle knowledge accumulation from other age-correlated processes such as cortical maturation when studying age differences in memory retrieval (Brod, Lindenberger, & Shing, 2016)? (b) Is the female menstrual cycle associated with changes in the volume and functional connectivity of the hippocampus (Lisofsky, Mårtensson et al., 2015)? (c) How can we build a unified statistical framework for the study of within-person and between-person structures (Voelkle, Brose, Schmiedek, & Lindenberger, 2014)? (d) How can we help researchers in the a-priori identification of longitudinal research designs that optimize the statistical power to detect individual differences in change (Brandmaier, von Oertzen, Ghisletta, Hertzog, & Lindenberger, 2015)? We provide our current answers to these questions and many more on the following pages.
Research Project 1: Cognitive and Neural Dynamics of Memory Across the Lifespan (ConMem)

The overarching objective of the ConMem project is to provide mechanistic explanations for developmental changes and interindividual differences in various aspects and functions of memory, with an emphasis on episodic and working memory. The project proceeds on the assumption that lifespan changes in memory functioning can be mapped onto the interacting contributions of two components, one associative and the other strategic. The associative component of memory refers to mechanisms that bind different aspects of an event into a cohesive memory representation and can be linked to medio-temporal areas (especially the hippocampus, HC) as well as posterior association areas. The strategic component refers to attentional and control processes that aid and regulate memory functions and is mainly supported by prefrontal and parietal regions. Interactions among maturational, experience-dependent, and senescent forces shape the relative contributions of associative and strategic processes during memory encoding, consolidation, and retrieval.

The heuristic value of this framework for understanding lifespan age differences in episodic and working memory has been empirically validated in a series of behavioral, functional imaging (fMRI), and electroencephalographic (EEG) studies (e.g., Fandakova, Sander, Werkle-Bergner, & Shing, 2014; Sander, Lindenberger, & Werkle-Bergner, 2012; Shing, Werkle-Bergner, Brehmer, Müller, Li, & Lindenberger, 2010).

Age Differences in the Interplay Between Associative and Strategic Components: Modulation by Memory Strength at Encoding, Consolidation, and Retrieval

Not all mnemonic events are equal. Some are encountered only once, but are vividly remembered throughout life. By contrast, other events occur repeatedly without leaving any recoverable trace. Do aging-related changes in prefrontal and medio-temporal regions weaken memory traces formed in old age? Do younger and older adults differentially rely on associative and strategic processes when forming new memories? Do mechanisms contributing to memory consolidation during sleep differ by age?

To address these questions, we designed the MERLIN Study, which allows us to track the mnemonic strength of single events within a given person (for details, see Figure 5). The study consisted of a multisession protocol including behavioral, EEG, and MRI assessments, as well as ambulatory polysomnographic sleep monitoring in half of the sample. It was conducted from July 2013 to July 2015. Based on the data from this study, we are currently investigating whether age differences in the elaboration of learned scene–word pairs contribute to age differences in episodic memory performance. Preliminary results demonstrate that during initial encoding, decreases in rhythmic neural alpha activity (~10 Hz) gradually track differences in memory strength, suggesting that prolonged alpha desynchronization during encoding enables deeper semantic elaboration on individual items. Younger and older adults show qualitatively similar effect patterns, suggesting that successful encoding depends on comparable neural mechanisms across the entire adult age range. Age-associated decrements in memory performance most likely result from a decreased propensity to reliably implement similar sets of mechanisms.

Sleeping after learning benefits memory, but with advancing adult age, both sleep and memory performance tend to deteriorate. By assessing memory strength at the item level within each study participant, we seek to disentangle the effects of reduced overnight forgetting from active enhancement of initially labile memory traces (Dissertation Beate E. Mühlroth). First analyses conducted in collaboration with Björn Rasch (University of Fribourg, Switzerland) show that overnight memory enhancement was of similar magnitude in both age groups, whereas forgetting was more pronounced in older adults. Despite
Day 1: Age-adapted repeated learning paradigm

A  Study  B  Cued recall & feedback  C  Criterion cued recall

YA: 440 pairs, 1 x phase B
OA: 280 pairs, 2 x phase B

Day 2: Delayed recall & recognition

D  Cued recall (only in Experiment 2)
E  Recognition (Experiment 1 & 2)

Experiment 2:
Sleep recordings in the nights before and after learning using ambulatory polysomnography (PSG)

Classification of pairs based on Day 1 retrieval success

High-strength pairs
Low-strength pairs

Ambulatory polysomnography (PSG)
PSG raw data
Identifying differences in individual sleep profiles

(a) Younger adults
Older adults

Proportion false recognitions

(b) Left insula and hippocampus
Left anterior cingulate

Figure 5. MERLIN Study design. Upper panel: Participants studied scene–word pairs using an imagery-based memory technique (Day 1). After first presentation, each image served as a cue for participants to recall the associated word. Regardless of recall accuracy, the correct word was presented again, allowing further associative learning. A final cued-recall task without feedback (Day 1, C) served to classify the items as high-versus low-strength pairs for a recognition test on Day 2 (Experiment 1). Learning was monitored with EEG and retrieval was assessed with fMRI. In a new sample, we used the same paradigm, with delayed cued recall instead of recognition, and monitored sleep in the nights before and after learning (Experiment 2). Middle panel: Ambulatory polysomnography (PSG) allows monitoring of neurophysiological sleep patterns at home. Manual scoring of sleep stages revealed less time spent in deep sleep and more fragmented sleep in older than in younger adults. Lower panel: Initial analyses show increased proportions of false recognitions in older adults, specifically for high-strength scene–word pairs. Apparently, they experienced greater difficulties in identifying new combinations of overlearned material. This effect was associated with altered neural activity in insular cortex, hippocampus, and anterior cingulate.

© MPI for Human Development
altered sleep architecture in older adults, there were no age differences in the association between sleep physiology and memory performance. Slow wave activity and the occurrence of sleep spindles were related to overnight forgetting in both age groups. Older adults are more likely than younger adults to form partially or entirely false memories of past episodes. In collaboration with Roberto Cabeza (Duke University, USA), we sought to delineate the neural correlates of this particular pronounced age difference. While there were no age differences in false memory for low-strength pairs, older adults were also more likely to falsely endorse high-strength pairs. False recognition engaged cingulo-opercular regions. Activity in these regions increased for low-strength pairs in younger, but not older, adults, indicating age-related deficits in retrieval monitoring. We found no age differences in HC activity, which was higher for correct recognition of high-strength pairs. Higher cingulo-opercular and HC activity predicted lower false memory rates in younger and older adults, suggesting that binding and monitoring mechanisms contribute to false memory complementarily.

**HC Subfield Contributions to Memory Development**

Adaptive learning systems need to meet two conflicting goals: detecting regularities in the world through generalization versus remembering specific events through disambiguation—functions implemented in the 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 the contribution to generalization and specification in cognitive development remains elusive. By using high-resolution in-vivo MRI data from children (6–14 years) and younger adults, 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 (see Figure 6). 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.

--

**Figure 6.** High-resolution structural MR images were acquired to study the contributions of maturational changes in hippocampal subregions to memory development. Trained raters manually identified boundaries between subfields. By combining subfield boundaries along the long axis of the HC, volumes were estimated based on three-dimensional models (shown on the right for the four traced subregions).

© MPI for Human Development
Age Differences in the Influence of Prior Knowledge on Memory
Prior knowledge influences memory functioning (Dissertation Garvin Brod). We showed that knowledge improves memory by facilitating binding in the HC and enhancing its communication with the association cortices (Brod, Lindenberger, Wagner, & Shing, 2016). To disentangle knowledge accessibility from availability, we developed a paradigm that induces equal amounts of artificial knowledge in younger adults and children. We showed that the medial versus lateral prefrontal cortices support successful retrieval of information that is congruent versus incongruent with prior knowledge, respectively (Brod, Lindenberger, Werkle-Bergner, & Shing, 2015). Furthermore, children aged 8 to 12 years showed less medial prefrontal, but similar HC activation as younger adults when retrieving information successfully (Brod, Lindenberger, & Shing, 2016). This is in line with the two-component model of episodic memory development (Shing et al., 2010) proposing a developmental shift from HC-bound processing to increasing recruitment of prefrontal cortex in the service of memory.

Age Differences in the Interplay of Attention and Memory
Memory is tightly modulated by attention. However, the contributions of age differences in attention to memory are not well understood. The modulation of attention is linked to the functionality of the noradrenergic system as well as rhythmic neural activity in the alpha frequency range. To reveal their interplay and alterations with advancing age, we conducted a multimodal assessment (Dissertation Martin J. Dahl) of the structural and functional integrity of the central noradrenergic system (via neuromelanin-sensitive MRI and pupilometry respectively) and of rhythmic neural activity (via simultaneous EEG). Our ultimate aim is to derive a mechanistic understanding of age-related declines in attention by revealing the interplay between the noradrenergic system and rhythmic neural activity within persons. This study is conducted in collaboration with Mara Mather (University of Southern California, USA).

Extending the Toolbox of Developmental Memory Research
Cognitive neuroscience aims to establish general laws that validly describe the multiple mappings between neural processes and behavior for any individual. The heterogeneity of these mappings within and across individuals poses methodological and conceptual problems, which are exacerbated by lifespan changes in neural resources and behavioral repertoires. So far, between-person differences are often treated as “noise” that can be suppressed by averaging across persons. However, if individuals deviate from the “mean model” in significant ways, inferences derived from group studies may be misguided. As a principled alternative, we attempt to reliably identify neural and behavioral processing parameters at the within-person level. To this end, we explored the potential of massively repeated assessments (Dissertation Thomas H. Grandy) in conjunction with advanced statistical pattern recognition techniques (see Figure 7; cf. Karch, Sander, von Oertzen, Brandmaier, & Werkle-Bergner, 2015) to estimate person-specific parameters of processing dynamics as a viable and sound basis for generalizations across persons. This line of research is pursued in close collaboration with the Formal Methods project (see pp. 172–174).

Key References
Figure 7. The current focus of spatial attention can be decoded with good precision from rhythmic neural EEG activity in the alpha frequency range (~10 Hz) in children, younger, and older adults. The sources of neural activity used for classification differ across age groups, as illustrated in the topographical distributions on the left. Decoding accuracy is lowest in children, but comparably high in younger and older adults, possibly suggesting higher consistency of task-based neural patterns in adults (middle graph). Inspection of the onset time points and the duration of time frames related to each participant’s best classification accuracy reveals differences in the temporal emergence of discriminatory neural activity (graph to the right). High decoding accuracy for children and adults can be achieved across the entire poststimulus period. In older adults, activity specific to attentional focus is mainly found early on after stimulus onset, most likely reflecting a greater reliance on bottom-up processing (adapted from Karch, Sander, von Oertzen, Brandmeier, & Werkle-Bergner, 2015).

© MPI for Human Development

Minerva Group (led by Yee Lee Shing)

Delineating Environmental Effects on Brain and Cognitive Development

The overarching goal of this group is to better understand the mechanisms through which environmental factors, such as school entry and stress-related social disadvantage, may affect neural and behavioral development. The HippoKID Study longitudinally followed children born close to the cut-off date for school entry who subsequently did or did not enter school that year. Schoolchildren displayed larger behavioral improvements in cognitive control than kindergarteners and also showed increased activation in posterior parietal cortex, a region important for sustained attention, while performing an inhibitory control task (Brod, Bunge, & Shing, 2017). In contrast, longitudinally observed improvements in episodic memory did not differ reliably between the two groups, suggesting that formal school entry primarily promotes brain mechanisms that help children to focus on cognitively demanding tasks. The ongoing longitudinal Jacobs Study aims to elucidate the roles of glucocorticoid and inflammation signaling in mediating the effects of stress on neural and behavioral development while assessing moderators at multiple levels, including (epi-)genetic dispositions (Dissertation Laurel Raffington).

Box 1.

Minerva Group (led by Myriam C. Sander)

Age Differences in Memory Representations

Established in 2016, this research group aims at understanding how aging affects memory representations and performance. Memories are encoded in distributed patterns of neural activity that are reactivated during later recall. To promote accurate retrieval, patterns representing different memories should differ from one another, whereas patterns representing several instances of the same memory should be similar to each other. To render memories durable, newly encoded patterns are spontaneously reactivated and strengthened during rest and sleep periods. The group will investigate how normal aging affects the distinctiveness and similarity of memory representations during memory formation and retrieval (Dissertation Verena R. Sommer). A related line of research will target age differences in the spontaneous reactivation of memories during rest.

Box 2.
Research Project 2: Mechanisms and Sequential Progression of Plasticity

This project addresses the questions of whether and how plasticity contributes to adult development. Special attention is given to the relationship between neural and behavioral manifestations of plasticity. Simone Kühn was the main principal investigator of this project from 2013. She was awarded a Heisenberg Professorship (W3) at the University Medical Center Hamburg-Eppendorf (UKE), where she is continuing her work from 2017 onward. In October 2016, Yana Fandakova and Elisabeth Wenger became the co-heads of this project.

The human brain has a significant capacity to adapt to changing environmental demands by altering its function and structure (see Lövdén, Wenger, Mårtensson, Lindenberger, & Bäckman, 2013). The central goals of this project are to delineate the mechanisms and sequential progression of behavioral and neural plasticity across the lifespan. The guiding propositions of the project are based on the assumption that plasticity is induced by a mismatch between environmental demands and an individual’s current behavioral and neural resources (see Figure 4, p. 145). The project is interested in plastic changes across the lifespan, induced by mismatches in either direction: It examines situations in which current demands exceed supply (e.g., cognitive interventions) as well as situations in which supply exceeds current demands (e.g., sensory deprivation). Training studies targeting specific brain regions and circuits that hypothetically support particular skills are central to the project’s research agenda. In addition, the project also examines plasticity in real-life contexts that are likely to induce a mismatch between demand and capacity. Furthermore, examining individuals who are experts in particular skills offers yet another window on the consequences and correlates of plasticity. In the following, we provide a selective summary of completed studies, ongoing work, and future plans.

Skilled Motor Performance

Skilled motor performance provides a rich testing ground for exploration of the mechanisms and progression of plasticity. 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 et al., 2017). After 4 weeks, we observed increases in gray matter in both left and right primary motor cortices relative to a control group; another 3 weeks later, these differences were no longer reliable (see Figure 8). Time-series analyses showed 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. The regions of observed structural change are in close vicinity to anatomical hand knobs that are easily discernible on anatomical MR images and also lie within regions of functional activation maps for left- and right-hand finger tapping and left- and right-hand writing inside the scanner.

Spatial Navigation

Following up on a series of studies investigating the influence of spatial navigation training on brain structure, we have reported gray matter increases in the right prefrontal cortex, the right hippocampal formation, and in both hemispheres of the cerebellum after daily playing of a commercially available video game in which participants had to navigate an avatar through a 3D world (Kühn, Gleich, Lorenz, Lindenberger, & Gallinat, 2014).

An ongoing study examines scientists who are spending 15 months at the Neumayer Station of the Centre of German Research in Antarctica. Before the scientists leave for their extended stay in an environment that is generally devoid of spatial cues, we assess their spatial abilities and acquire high-resolution structural images of the hippocampus. MR imaging assessment is repeated after the scientists return from Antarctica to examine whether the spatially poor environment in Antarctica is associated with declines in spatial abilities and related brain structures, and whether these declines are reversible. Data acquisition of two cohorts of participants is now

Key References


Researchers

Yana Fandakova (as of 10/2016)
Simone Kühn (until 02/2017)
Elisabeth Wenger Ulman Lindenberger Martin Lövdén
Elisa Filevich (until 08/2015)
Johan Mårtensson (until 02/2014)
Markus Weichenberger (until 12/2014)
Oisin Butler (as of 04/2014)
Neda Khosravani (as of 10/2016)
Nina Lisofsky (until 06/2016)
completed, and initial results show decreases in dentate gyrus volume of the hippocampus.

**Hormonal Influences on Brain Plasticity**

The brain is subject to hormonal influences, which may affect plasticity. Hence, the project has investigated the influence of gonadal hormones, in particular estrogen and progesterone, on brain structure and function in women (Dissertation Nina Lisofsky). To explore the existence of structural changes, we scanned participants at four time points distributed across the menstrual cycle. We observed a bilateral increase in posterior hippocampal volumes during the late follicular phase when estrogen is at its peak, relative to the early follicular phase when estrogen is low (Lisofsky, Lindenberger, & Kühn, 2015). A second study explored the effects of hormonal contraceptive use on brain structure. We found a decrease in gray matter in left amygdala extending into parahippocampal gyrus in women who used hormonal contraceptives (Lisofsky, Riediger, Gallinat, Lindenberger, & Kühn, 2016; see Figure 9). In a third study, we focused on the effects of pregnancy on brain and behavior. When comparing peripartal women with age-matched controls, we observed that pregnant women had lower performance in an egocentric navigation condition (associated with striatal integrity), but did not differ in an allocentric navigation condition associated with hippocampus integrity. In line with this behavioral difference, we found smaller left striatal volumes in peripartal women (Lisofsky, Wiener et al., 2016).

**Effects of Stress on the Brain**

In collaboration with Jürgen Gallinat from Charité Universitätsmedizin Berlin and with Peter Zimmermann and Gerd Willmund from the Bundeswehr Krankenhaus Berlin, we investigated plasticity in response to traumatic and stressful events as well as the development of posttraumatic stress disorder (PTSD) (Dissertation Oisin Butler). Soldiers being deployed to areas such as Afghanistan, Mali, and Kosovo were assessed before and after their mission on a range of psychological and brain imaging measures. A specific aim of the study is to find out whether differences in hippocampal structure or function are a risk factor for stress and trauma or rather a consequence thereof (Butler et al., 2017; see Figure 10).
Music and the Brain
Musical expertise is another suitable model for investigating structural plasticity of sensory processing in humans. In this ongoing line of work, we target the domain of auditory processing and investigate experience-induced changes in pitch processing. We recruited young adults who had signed up for a course that prepares candidates for the music conservatory entrance examination. An important component of this training course is relative pitch discrimination, that is, the ability to identify tones and intervals in relation to a reference tone. As a control group, we recruited younger adults who had received musical training in their youth and also performed music actively in their daily lives, but did not enroll in a preparatory course. All participants were assessed behaviorally and with functional and structural MRI 4 to 5 times in 10 to 12 months. In preliminary analyses, we found that aspiring professionals, but not amateurs, show a longitudinal gray matter decrease in left superior temporal gyrus.

Brain Structure and Metacognition
In a separate line of research, Elisa Filevich and colleagues have been investigating the association between brain structure and higher-order cognitive functions. Here, the project is particularly interested in metacognition, or the ability to know what one knows, and how this knowledge is related to introspection and interoception. In this context, we examined lucid dreamers as putative experts, as these individuals appear to be aware while dreaming (Filevich, Dresler, Brick, & Kühn, 2015). We assume that metacognition matters to plasticity by contributing to the demand–capacity mismatch representation that triggers a plastic response.

Berlin Aging Study II (BASE-II):
Magnetic Resonance Imaging
In addition to the core data acquisition of the Berlin Aging Study II (BASE-II; see the Berlin Aging Studies project, pp. 160–162), we acquired MRI data of 345 older and 100 younger participants in 2013 and 2014 in collaboration with Sandra Düzel. A first set of publications based on these data has been submitted. In 2015/16, participants were reinvited to complete a cognitive test battery and brain imaging measures. In early 2017, two waves of imaging data were available for 227 older and 60 younger BASE-II participants.

Further Collaborations
Together with Torsten Schubert from Humboldt-Universität zu Berlin and Jürgen Gallinat from Charité Universitätsmedizin Berlin, we compared simultaneous interpreters with consecutive ones and with translators to delineate the functional and structural neural correlates of dual-task performance (Becker, Schubert, Strobach, Gallinat, & Kühn, 2016; Strobach, Becker, Schubert, & Kühn, 2015). In an additional project, we conducted a dual–task working-memory training study (Salminen, Kühn, Frensch, & Schubert, 2016; Salminen, Mårtensson, Schubert, & Kühn, 2016).

In collaboration with Martin Dresler from the MPI for Psychiatry, Munich, Dimitris Repantis from Charité Universitätsmedizin Berlin, and Kathrin Ohla from the German Institute of Human Nutrition, Potsdam, we directly compared cognitive and neural changes in response to various substances or interventions, such as glucose, caffeine, methylphenidate, modafinil, caffeine pills, and memory training (e.g., Kunath et al., 2016; Ullrich et al., 2015).

Key Reference

Figure 10. Military deployment correlates with smaller prefrontal gray matter volume and psychological symptoms. Longer military deployment is associated with smaller regional brain volumes in combat-exposed individuals. PTSD = posttraumatic stress disorder (adapted from Butler et al., 2017). © MPI for Human Development
Methodological Work

In close collaboration with the Brain Imaging Methods project (see pp. 169–171), we also conducted methodological work to better understand, calibrate, and refine MRI protocols. We critically evaluated the automatic segmentation tool FreeSurfer, which is commonly used to assess structural differences and changes of the hippocampus. We found that the properties of this tool vary by age group. In comparison to manual segmentation, FreeSurfer introduced a systematic age bias in the data, rendering its use in old age groups dubious (Wenger et al., 2014; see Figure 11). Typical MRI studies generally assume that brain structure and function are inherently stable unless an experimental intervention is applied. However, the stability of MR measures cannot simply be assumed, but must be empirically tested. Therefore, we have taken measures of brain structure and function on a day-to-day basis within the same individuals to explore whether daily fluctuations in brain imaging parameters are related to fluctuations in physiological and affective states. Initial results from this study are currently under review.

Figure 11. The automatic segmentation tool FreeSurfer generally overestimates hippocampal volumes in comparison to manual segmentation, the “gold standard” method. Panels (a) and (b) show visualizations of (a) a smaller and (b) a larger manually segmented volume of the hippocampus in older adults (in yellow) and the additional voxels also labeled as hippocampal volume by FreeSurfer (in red). Critically, FreeSurfer overestimates larger hippocampal volumes in older adults (b) to a lesser extent than smaller hippocampal volumes (a), thereby introducing a bias in this age group (c) (adapted from Wenger et al., 2014).

© MPI for Human Development

Future Plans

Language Learning and Physical Exercise to Promote Healthy Aging

Physical and cognitive inactivity are important risk factors for age-associated cognitive decline in later adulthood, not only in neurodegenerative diseases but also in the normal (nonpathological) range of functioning. In recent years, it has been shown repeatedly that the structure of an adult brain can change in response to altered environmental demands. So far, however, little is known about the extent to which adoption of a physically and cognitively more active lifestyle in old age can positively influence brain structure and behavior. In a new intervention study with 160 healthy older participants, we are investigating whether the combination of cognitive and physical training boosts cognition and triggers plastic structural changes in healthy older adults more effectively than either type of training alone.

Mechanisms and Progression of Plasticity in Childhood

In a new line of research that started at the end of 2016, the project has begun to examine plasticity mechanisms in the context of child development. Childhood is characterized by maturational changes in brain structure and function and in the organization of behavior. We plan to explore age–graded and individual differences in plasticity resulting from intensive practice in task-set switching (Dissertation Neda Khosravani, in collaboration with Silvia Bunge, University of California, Berkeley, USA). With this line of research, we also seek to extend the observation of the temporal progression of behavioral and neural manifestations of plasticity to childhood and adolescence.

Key Reference

Research Project 3: Intra-Person Dynamics Across the Lifespan

The overarching objective of this project is to test theories and explore research designs that articulate human development across different timescales, levels of analysis, and functional domains. The project is based on the premise that a comprehensive understanding of behavioral development across the lifespan requires a person-oriented, multivariate, and longitudinal approach. Only a high density of observations within individuals allows researchers to distinguish among different forms and functions of variability and change, with the goal of delineating the dynamic properties of human behavior (e.g., flexibility, plasticity, fluctuation, and adaptability). Such high-density data 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 productive interplay between substantive research and method development. Regarding the latter, the project collaborates closely with the Formal Methods project (pp. 172–174). During the reporting period, the project focused on three domains of inquiry, summarized below.

Relationships Between Intraindividual Variability and Change Across Different Domains and Timescales

Investigations with data from the COGITO study (see Box 3) address intraindividual variability and change at timescales that range from moment-to-moment variability in reaction times, day-to-day fluctuations in cognitive performance, to changes over years—like the long-term effects of COGITO’s extensive cognitive training on cognitive abilities (Schmiedek, Lövdén, & Lindenberger, 2014b) and personality traits (Sander, Schmiedek, Brose, Wagner, & Specht, 2016). Analyses focus on the ways in which constructs are linked within persons over time, such as couplings between day-to-day fluctuations in positive affect and working-memory performance (Brose, Lövdén, & Schmiedek, 2014).

Special emphasis is placed upon attempts to explain individual differences in long-term change by individual differences in shorter term dynamics. For example, Hertzog, Lövdén, Lindenberger, and Schmiedek (in press) found that changes in performance on a paired-associates test of episodic memory from pretest to posttest were related to changes in strategy use during the training period. Self-reports on participants’ use of memory strategies at each of the 100 daily occasions showed that memory performance increased on occasions when such strategies were actually used. Persistent individual differences in the strength of these within-person couplings, which characterize the effectiveness of strategy use, predicted individual differences in performance gains.

Another example concerns the persistence of negative affect, often referred to as affective inertia (Brose, Schmiedek, Koval, & Kuppens, 2015), which is known to relate to depressive symptoms. Using COGITO data, we examined whether inertia is uniquely related to depressive symptoms after controlling for rumination. The consideration of rumination is highly relevant in this context because it is related to inertia and also plays an explanatory role in the etiology of depression. We used data from younger adults (N = 101) who provided ratings of affect and rumination for 100 days. Depressive symptoms were reported before and after the study. We found that day-to-day emotional inertia is indeed related to depressive symptoms beyond rumination. Moreover, inertia predicted changes in depressive symptoms from before to after the study even after controlling for its association with rumination, thereby establishing the independent relevance of emotional inertia for longer-term change in depressive symptoms.

Using Continuous Time and Moderated Time-Series Models to Analyze Human Development Across Different Timescales and Contexts

While most psychological processes develop continuously over time, we need to rely on discrete measurement occasions to infer them. The goal is thus to reconstruct the mecha-
nisms underlying a continuously unfolding process, such as human development, based on few discrete snapshots in time. In previous work, we have argued that continuous-time models are well suited to achieve this goal. As illustrated in Figure 12 and in contrast to popular discrete-time methods, continuous-time models link discrete-time observations to underlying continuous-time parameters by stochastic differential equations. This may not only remove bias due to variability in sampling time and improve comparability across different research designs; but it also yields valuable information about the nature of change. During the reporting period, we have continued this line of research and developed ctsem, an R package for continuous-time modeling that is freely available on the comprehensive R archive network CRAN (Driver, Oud, & Voelkle, 2017). In addition, we have developed a moderated time-series approach to incorporate context variables in traditional time-series models. Applying this approach to COGITO data, we are investigating changes in the dynamics of affect and stress, and how these depend on daily events. We plan to expand both lines of research by (i) adapting and applying the methods to different research domains, including youth development, personality development, and data from virtual environments that allow controlled environmental changes; and (ii) extending method development to higher-order continuous-time and non-Gaussian time-series models.

Key Reference


Figure 12. (a) Illustration of a bivariate continuous-time dynamic model. The model can be used to assess within-person dynamics on latent variables and, in this sense, is conceptually similar to autoregressive cross-lagged and bivariate latent change score models. However, the model uses stochastic differential equations to account for unequally spaced time intervals and incorporates information about heterogeneity across individuals by the inclusion of traits. Inferences on both simultaneous as well as lead–lag relationships among (latent) variables of interest are possible (see also Voelkle & Wagner, 2017). (b) In a continuous-time dynamic model, a set of continuous-time parameters are estimated, and these are combined with information about the time interval between observations to generate expected auto- and cross-regressive effects. This plot can also be understood as displaying the effects that would be expected if one had instead fit a discrete-time model, with a specific time interval between observations. (c) With the hierarchical Bayesian continuous-time dynamic models we are developing, an individual’s score on some covariate or set of covariates can be used to inform and predict the individual’s deviation from the population mean on all within-person parameters (such as the illustrated auto- and cross-effects).
Integrating Within-Person and Between-Person Information in the Search for Causal Mechanisms

Most empirical research in psychology is based on analyzing between-person variation. In contrast, most applied psychology is concerned with variation within individuals. In addition, the mechanisms specified by psychological theories generally operate within, rather than across, individuals. For example, we would like to make statements such as, “since she is so intelligent she can solve the equation,” implying that the counterfactual statement is also true. Usually, however, there is little empirical evidence for such a conclusion because what we typically observe are other people who are, or are not, able to solve the equation. This disconnect between research practice, applied demands, and psychological theories constitutes a major threat to the conceptual integrity of the field. Reactions range from ignoring the problem to calls for exclusively within-person research paradigms. The project is working on reconciling these extreme positions, both conceptually and methodologically. In particular, Voelkle, Brose, Schmiedek, and Lindenberger (2014) proposed the concept of conditional equivalence to study the commonalities of between-person and within-person structures by controlling for factors that may only affect the between-person or within-person structure. Likewise, using affect data from the COGITO study, Brose, Voelkle, Lövdén, Lindenberger, and Schmiedek (2015) showed that differences between within-person structures and between-person structures can be considered as a matter of degree. Currently, Driver and Voelkle are developing a hierarchical Bayes approach to dynamic modeling that attempts to optimally integrate information within and across individuals and time points in the context of continuous-time modeling. Our future work will continue in this direction, with an increasing emphasis on how to extract causal mechanisms from mixed between-person and within-person data structures.

Key References


In October 2016, the MPI for Human Development hosted the COGITO Conference 2016, entitled “The COGITO Study: Looking at 100 Days Ten Years After.” Its aim was to discuss methodological and conceptual implications of the COGITO study. World-leading scientists with a strong interest and expertise in methodology, individual differences, and adult development were invited to take a fresh look at COGITO. Importantly, the COGITO data set was made available to conference participants, who were encouraged to use these data for their own analyses and publications. Five of the 29 invited conference presentations have been suggested for submission to a special section on COGITO in the journal *Multivariate Behavioral Research*.

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, Lövdén, & Lindenberger, 2010). 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 3.**
Research Project 4: The Berlin Aging Studies (BASE)

During the 20th century, average life expectancy nearly doubled. More and more individuals in current generations of older individuals experience additional years of life between the ages of 70 and 100+. What do these added years mean in terms of levels of functional capacity and quality of life? What are the constraints on mental and physical capacities in the last years of life? Given the heterogeneity of aging trajectories and outcomes, longitudinal studies of individual development are crucial in providing answers to these questions (cf. Voelkle, Brose, Schmiedek, & Lindenberger, 2014).

For almost 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, Smith, Mayer, & Baltes, 2010). The Berlin Aging Study II (BASE-II; Bertram et al., 2014) was launched in 2013 to address antecedents of healthy aging. Both BASE and BASE-II are collaborative, multidisciplinary studies that involve researchers from other institutions inside and outside Berlin. In the following, we highlight select recent developments from both studies.

The Berlin Aging Study (BASE)

Longitudinal data in BASE are available for eight measurement occasions spanning more than 18 years, and mortality-related information is updated at regular intervals. Almost all of the 516 individuals who participated in the 14-session multidisciplinary assessment at the first measurement occasion about 25 years ago are no longer alive. BASE data continue to provide the basis for new original publications on individual differences in late-life development (e.g., Hilbrand, Coall, Gerstorf, & Hertwig, 2017).

Similarities between BASE and BASE-II (see below) allow for a direct evaluation of cohort differences in normal aging within relatively short periods of time.

The Berlin Aging Study II (BASE-II)

BASE-II is a multidisciplinary and multi-institutional longitudinal study capturing a wide range of different functional domains. At the first wave of measurements (T1), the sample of the study consisted of 1,600 participants aged 60 to 80 years and 600 individuals aged 20 to 35 years. Data collection for T1 was completed in 2014. In addition, eligible BASE-II participants (n = 445) were invited for magnetic resonance imaging (MRI) of the brain. The latter subsample was reinvited to a cognitive and psychosocial follow-up including a second MRI assessment from 2015 to 2016 (n = 327; see Figure 14). The MRI assessments of the BASE-II sample were conducted by the Plasticity project (see p. 155).

Within BASE-II, the goal of the Psychology Unit is to obtain a detailed and comprehensive picture of cognitive abilities and psychosocial characteristics. By relating individual differences in cognitive abilities and brain structure and their changes to differences in lifestyle, environmental factors, and personality, we seek to identify different patterns and psychosocial contexts of cognitive aging. Theories of motivation postulate that older individuals’ subjective appraisals of their remaining life time affects their goals and activities. BASE-II researchers newly developed and validated the Subjective Health Horizon Questionnaire (SHH–Q), which reliably assesses individual differences in four distinct dimensions of future time perspective. Two of these dimensions, Novelty and Body, were found to relate differentially to cognitive status and somatic health. Specifically, greater
self-reported future novelty orientation was associated with higher current memory performance, and greater future expectations regarding bodily fitness, with better current metabolic status (Düzel et al., 2016). We expect that the SHH-Q will help to identify antecedents, correlates, and consequences of an active lifestyle.

The cognitive battery of BASE-II is well suited for investigating associations between cognition and other functional domains. Ongoing analyses investigate cross-sectional and longitudinal links to genetic variation, metabolic load, vascular risk, and psychosocial characteristics.

Key References


Figure 13. Average cohort differences and individual differences in cognitive performance (a: Digit Symbol test) and indicators of well-being (b: morale; c: positive affect; d: negative affect). The dots represent raw data from participants in the matched BASE (n = 161; red dots) and BASE-II (n = 161, blue dots) samples. Sample means and standard errors for each cohort are displayed separately. Participants in the BASE-II cohort (data obtained from 2013 to 2014) showed higher levels of cognitive performance and well-being compared to the BASE cohort (data obtained from 1990 to 1993). The analyses suggest substantial secular improvements in cognition and well-being (adapted from Gerstorf et al., 2015).
© MPI for Human Development

Figure 14. Schema of BASE and BASE-II study designs.
* The brain imaging assessment of BASE-II participants was conducted by the Plasticity project (see p. 155).
© MPI for Human Development
Overview of the Berlin Aging Study (BASE)

The multidisciplinary Berlin Aging Study (BASE), initially directed by the late Paul B. Baltes and Karl Ulrich Mayer, was started in 1989. Ulman Lindenberger heads the current BASE research group. 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 (see also Delius, Düzel, Gerstorf, & Lindenberger, 2015). The core sample formed the basis of the cross-sectional analyses reported in two monographs (see Baltes & Mayer, 1999; Lindenberger, Smith, Mayer, & Baltes, 2010). Current work in BASE uses longitudinal data to address issues such as variability and change, mortality prediction, self-related change, and genetic predictors of cognitive change.

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

BASE-II investigates human development into old age and aims at identifying conditions and mechanisms that contribute to individual differences in cognitive, psychosocial and physical functioning (see Bertram et al., 2014; Gerstorf et al., 2016b). In doing so, it conceives of aging as a systemic phenomenon and seeks to delineate sources of heterogeneity in aging trajectories (Lindenberger, 2014). 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. The initial sample consists of 1,600 participants aged 60 to 80 years and 600 individuals aged 20 to 35 years. BASE-II includes molecular genetics and immunological methods and uses instruments from the German Socio-Economic Panel (SOEP), which provide information about participants’ socioeconomic background, lifestyle, and living conditions.

The Berlin Aging Study II: Steering Committee

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

Coordination
Katrin Schaar MPI for Human Development, Berlin (until 12/2015), Humboldt-Universität zu Berlin, Germany (as of 01/2016)
Research Project 5: Interactive Brains, Social Minds

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 15).

The project continued its major focus on analyzing electroencephalographic (EEG) data of skilled musicians playing music together (see Figure 16). In our initial study with guitar duets, we discovered that interpersonally co-ordinated actions are preceded and accompanied by within-brain synchrony and between-brain oscillatory couplings (Lindenberger, Li, Gruber, & Müller, 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, we found that within-brain connections tend to operate at higher frequencies (e.g., beta, gamma) than between-brain connections (e.g., delta, theta)—in line with researchers

Viktor Müller
Ulman Lindenberger
Timothy R. Brick
Dionysios Perdikis
Caroline Szymanski

Key References

© MPI for Human Development
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).

In a methodologically oriented reanalysis of standard single-person EEG data during rest and auditory oddball performance (Müller et al., 2016), we showed that cross-frequency couplings (CFC), in addition to within-frequency couplings (WFC), help to characterize the topology of hyper-frequency networks, including condition differences in graph-theoretical parameters, such as strength, clustering coefficient, characteristic path length, as well as local and global efficiency.

We explored the utility of hyper-frequency, hyper-brain networks in a data set of couples engaged in romantic kissing (Müller & Lindenberger, 2014). Oscillations in the alpha band played a central role in binding the two brains together. Also, 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 went back to cardiac, respiratory, and vocalizing data from 11 singers and 1 conductor engaged in choir singing (Müller & Lindenberger, 2011). Ongoing analyses reveal that 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. The conductor’s hand movements are synchronized with each of the three subsystems.

In a second line of work, the project has sought to devise new EEG paradigms that are suited to delineate the behavioral function of inter-brain synchrony (Dissertation Caroline Szymanski). In one of these studies (Szymanski 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 constitutes a neural correlate of social facilitation and may help to explain why some teams perform better than others. A second study tests the hypothesis that same-frequency, same-phase transcranial 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. The collected data are currently being analyzed.
Figure 17. Coupling strengths and connectivity brain maps while playing guitar in a quartet. (a) Guitar traces in the four guitarists and the four time windows represented by the brain maps. (b) Time course of within- and between-brain out-strengths in the four guitarists. (c) Brain maps of within-brain connectivity in the four guitarists across the four time windows shown in (a). (d) Brain maps of between-brain connectivity in the four guitarists across the same four time windows. Note that color in (a)–(d) corresponds to the different guitarists as depicted in (a). During the first time window, when guitarist D (shown in yellow) is playing alone, strong within- and between-brain connectivity is evident. (e) Modularity structures of hyper-brain networks across the same time windows. Modules are coded by color. Note that most are hyper-brain modules sharing nodes from two, three, or even four brains.

© MPI for Human Development
Research Project 6: Sensorimotor–Cognitive Couplings

Goal-directed behavior requires the seamless integration of perception, movement, and thought. Examples include the simultaneous performance of cognitive and motor tasks, the coordination of elementary body movements, and action planning. The project investigates how infants construct these integration skills and how they further evolve across the lifespan.

The Movement Lab, in which most of our research takes place, is equipped with a motion capture system allowing us to measure the positions of reflective markers attached to a participant’s body with high temporal and spatial accuracy (see Figure 18). Motion capture can be combined with synchronized measurements of ground reaction forces control or muscle activity. The Lab is also equipped with a multichannel video system for behavioral studies with infants.

Coordination of Cognitive and Motor Performance in Dual-Task Situations

When a cognitive and a motor task need to be performed concurrently, older adults often show higher dual-task costs than younger adults and tend to prioritize the motor domain (Schaefer, 2014). However, we found that this prioritization may function less effectively in older relative to younger adults when multiple challenges are combined (Schaefer, Schellenbach, Lindenberger, & Woollacott, 2015). In our study, participants walked on a speed-adaptive treadmill as fast as possible through four different virtual environments: broad or narrow tracks; on ground level or an elevated level (see Figure 19). Young adults maintained their walking speed and kept the number of missteps low, even when walking on an elevated narrow track while performing a challenging working-memory task. In contrast, older adults actually increased their walking speed on elevated relative tracks and committed more missteps under cognitive load. In the real world, this strategy may be maladaptive and result in falls. We also investigated the influence of walking speed and cognitive load on gait regularity in children aged 7 or 9 years and young adults (Schaefer, Jagenow, Verrel, & Lindenberger, 2015). In all age groups, regularity of lower body coordination increased with walking speed. Children showed a U-shaped relationship between cognitive load and walking regularity, with the highest regularity in the easy cognitive task. In contrast, young adults’ gait regularity was not influenced by cognitive load. These results indicate that the effects of cognitive load on motor performance are modulated by age, similar to what we observed in an earlier study comparing younger and older adults.

Interaction of Cognitive and Motor Task Components

Cognition and motor control also interact when cognitive tasks require a complex motor response. We investigated the influence of response conflict on movements requiring a postural preparation in form of a weight shift, namely, lifting one foot from the floor in a standing position while ignoring visual distractors priming the same or the opposite response (see Figure 20a). Under balance...
constraints, young adults showed automatic imitation tendencies for whole-body movements (Verrel, Lisofsky, & Kühn, 2014). In a subsequent age-comparative study (Verrel, Lisofsky, Kühn, & Lindenberger, 2016), older adults responded more slowly than younger adults, whereas stimulus-compatibility effects did not differ reliably by age (see Figure 20b). Compatibility effects as well as age differences in response latency were associated with postural preparation errors, pointing to erroneous response activation as their potential source. In ongoing studies, we seek to delineate the points in the action hierarchy, from goals to movement execution, at which these compatibility effects originate.

Movement Coordination, Anticipatory Control, and Action Planning

Motor behavior requires the coordination of multiple body parts to achieve desired action outcomes. We introduced a novel method that estimates interjoint coordination by quantifying the effect of artificially eliminating movement at individual joints. Applying this “freezing” method to the coordinative skill of cello bowing revealed pronounced differences between novices and expert cello players, especially for the wrist and elbow (Verrel, Woollacott, & Lindenberger, 2014). Our results emphasize the importance of coordination across multiple joints, in particular distal joints, for skilled motor performance.

Anticipatory control and advance planning are defining features of motor action. In collaboration with Karen Adolph (New York University, USA), we have begun to investigate anticipatory adjustments to locomotor movements in young infants crawling over small obstacles (see Figure 18b). Preliminary results indicate that infants use visual and haptic information for anticipatory adjustments of locomotion. In contrast to results from animal studies, however, anticipation was found to be unstable, showing high intra- and interindividual variability. Currently, we are investigating decision making, advance planning, and motor coordination in infants aged 10 to 16 months when confronted with height challenges that vary in difficulty (see Figure 18c). In particular, we explore how flexibly and adaptively infants use alternative strategies, such as descending via a sitting posture, sideways or backward, and to what extent these strategies generalize across environmental conditions, such as steps versus slopes, and across locomotor styles, such as crawling and walking.

Key References


Effects of Physical Exercise on Brain and Behavior

In close collaboration with the Plasticity project (pp. 153–156), we conducted an exercise intervention study to identify physiological mechanisms that may elucidate the positive association between regular physical activity on cognitive performance in old age. Fifty-two older adults exercised on bicycle ergometers for 6 months three times a week. Changes in fitness were associated with changes in hippocampal tissue density (measured by mean diffusivity), which in turn were associated with changes in hippocampal volume. These results suggest that fitness-related changes in hippocampal volume may be driven by an increase in cell membranes (Kleemeyer et al., 2016). In addition, we found a positive association between changes in fitness and changes in the specificity of neural responses to visual stimuli (see Figure 21; Kleemeyer et al., 2017), suggesting that regular physical exercise can help maintain neural specificity in older adults. In ongoing analyses of this data set, we examine whether changes in white matter and cerebral blood flow are associated with exercise-induced fitness changes.

Figure 20. Response conflict in whole-body movements with balance constraints. (a) Exemplary stimuli (Verrel, Lisofsky, Kühn, 2014; Verrel, Lisofsky, Kühn, & Lindenberger, 2016). Participants responded to the symbolic stimulus (L or R) by lifting their left or right foot off the floor. Visual distractors showed a congruent or incongruent movement. (b) Response times for young and older adults. Postural preparation errors showed an analogous pattern, and differences in response times between conditions and age groups were largely explained by erroneous postural preparation (adapted from Verrel, Lisofsky, Kühn, & Lindenberger, 2016).

© MPI for Human Development

Key References


Figure 21. Relation between physical fitness and brain function. Scatter plot displaying a significant association between changes in fitness and changes in neural specificity, that is, the degree to which neural representations of different visual stimuli (e.g., faces and houses) can be discriminated by means of multivariate pattern analysis (adapted from Kleemeyer et al., 2017).

© MPI for Human Development
Research Project 7: 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. Magnetic resonance imaging (MRI) and magnetic resonance spectroscopy (MRS) have become indispensable tools in this context, as they allow noninvasive assessment of brain function, anatomy, microstructure, and metabolism.

The two main goals of the Brain Imaging Methods project are: (i) to ascertain and improve the measurement quality of standard brain imaging protocols at the Center; (ii) to 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., Kleemeyer et al., 2016; Wenger et al., 2017).

Structural and quantitative MRI methods occupy a central place in the project. During the reporting period, the project has focused on (i) high-resolution T1-weighted imaging to obtain estimates of volume or thickness of specific substructures of the brain; (ii) diffusion imaging and multiparametric mapping (MPM) to obtain brain maps that permit quantitative estimates of histological parameters; (iii) susceptibility-weighted imaging to obtain maps of mineralization, especially for the brain’s deep gray matter structures; and (iv) myelin water fraction (MWF) imaging by mapping the fraction of shortest T2 relaxation rates quantitatively. The latter method provides an estimate of the portion of water molecules located between myelin sheaths, presumably reflecting the degree of myelination within white matter. Work on MPM profits from collaboration with Nikolaus Weiskopf (MPI for Human Cognitive and Brain Sciences, Leipzig, Germany).

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: (i) high-resolution functional imaging of the hippocampus; (ii) task-related, time-resolved applications of proton MRS, with a focus on glutamate and GABA; and (iii) phosphorus MRI to capture individual differences in brain metabolism. Work in this area involves collaborations with Mara Mather (University of Southern California, Los Angeles, USA), Florian Schubert (Physikalisch-Technische Bundesanstalt, Berlin, Germany), and Jeff Stanley (Wayne State University, Detroit, USA).

In the following, we provide additional details on three of the methods that have been the focus of our attention during the reporting period.

Diffusion Imaging

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 less hampered along than across fiber tracts. Diffusion within a voxel (a three-dimensional data point) is often captured by a tensor (ellipsoidal) model. However, by permitting only one directional description per voxel, diffusion tensor imaging provides an impoverished, and at times inaccurate, picture of histological reality; for instance, the crossing of fibers may go unnoticed. To enhance the microstructural veridicality of diffusion imaging, the project is working on multishell diffusion imaging acquisition schemes to improve the precision of orientational information. Diffusion models under scrutiny are the sticks-and-ball model (used by FMRIB Software Library, FSL), constrained spherical deconvolution (implemented in MRtrix), and physiologically motivated multicompartment models (e.g., neurite orientation dispersion and density imaging, NODDI). We plan to use multishell diffusion imaging in combination with nontensor diffusion modeling to move toward a more...
precise picture of age- and training-related changes in the brain’s structural connectivity.

Quantitative Multi-Parameter Mapping (MPM)
Normal aging is accompanied by characteristic changes in the brain’s morphology and microstructure. Quantitative MRI can help in characterizing the brain’s microanatomy by using the physical properties of water that govern the MRI contrast as surrogate parameters to describe tissue properties. Nikolaus Weiskopf, Gunther Helms, and colleagues have developed a comprehensive quantitative multiparameter mapping approach, which provides high-resolution maps of the longitudinal relaxation rate ($R_1 = 1/T_1$), effective proton density ($PD^*$), magnetization transfer (MT), and effective transverse relaxation rate ($R_2^* = 1/T_2^*$) (see Figure 22 showing exemplary maps for one subject examined in our project). In collaboration with the Plasticity project (pp. 153–156), we are currently investigating the reproducibility of MPM parameters within and across measurement occasions. For instance, we have acquired data from 15 volunteers, each measured four times on two consecutive days, either with or without repositioning, to tease apart various factors affecting reproducibility.

Phosphorus MRI
The mitochondria are organelles in eukaryotic cells that provide energy for the cell’s metabolism through glycolysis (i.e., the releasing of energy stored in glucose). Adenosine triphosphate (ATP) is generated during glycolysis for high-energy short-time storage. ATP concentration levels are stabilized by the creatine kinase (CK) reaction, which buffers ATP. Phosphocreatine (PCr) markedly varies with energy metabolism. Mapping changes in PCr concentration in brain tissue can thus be used to calculate an index of the brain’s energy metabolism in response to short-term peaks in energy demand. During the report-
ing period, the project has developed two different variants of a spectrally selective 3D turbo spin echo (TSE) imaging sequences that selectively excites PCr (Enggruber & Kreis, 2015). One sequence version allows for the functional (i.e., temporally resolved) task-related acquisition of the PCr concentration, whereas the other is designed to generate maps of the kinetic rate of the CK reaction by using selective saturation of the gamma ATP peak (see Dissertation Julian Q. Kosciessa in Lifespan Neural Dynamics Group, p. 199). In collaboration with Jeff Stanley, the project is working on establishing phosphorus MRI as a technique that may allow researchers at the Center to study individual differences in cerebral energy consumption as a function of age and other person characteristics.

The Magnetic Resonance Imaging Laboratory
The Institute operates a Siemens TIM Trio tomograph, which has a field strength of 3 Tesla. The MR system is equipped for proton (¹H) MRI and MRS with 12-channel and 32-channel head radio frequency coils, and a circularly polarized birdcage headcoil. Instrumentation for phosphorus (³¹P) MRS, that is, a dual-tuned circularly polarized head coil, a dual-tuned surface coil, and an additional high-frequency amplifier working at the resonance frequency of phosphorus, is also available. Additional components include a transcranial magnetic stimulation system with an MR-suited stimulation coil; an MR-suited EEG system; an audio/video stimulus presentation system using headphones and goggles; a visual presentation system based on video projection, mirrors, and a screen; an MR-compatible eye-tracking system; and a variety of hand-held response boxes for children and adults. The laboratory also houses a mock (i.e., fake) scanner that looks and sounds just like the real scanner. The mock scanner is used to familiarize research participants, in general, and children, in particular, to the scanning environment. As of March 2017, the core MR team consists of Sonali Beckmann (head of the MRI Measurement Facility), Nils C. Bodammer (physicist), Thomas Feg (technician), Davide Santoro (physicist), Sebastian Schröder (technician), and Nadine Taube (technical assistant). The team provides scientific and technical support for all MR imaging activities at the Institute.
Research Project 8: 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 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 Formal Methods project is dedicated to developing multivariate mathematical, statistical, and computational research tools that accommodate complex research designs with multimodal assessments collected over a wide range of timescales. It seeks to provide practical solutions to the methodological challenges of lifespan research and related fields of scientific inquiry. Its main goals are to critically examine the link between theory and data and equip researchers with means to improve the efficiency of data acquisition and data analysis.

The project is particularly interested in analyzing individual differences in longitudinal change. Hence, the project has further broadened its interest in Structural Equation Modeling (SEM) methods, which integrate a wide range of different multivariate analysis techniques. During the reporting period, project members have shown how SEM as a formal language can assist researchers in: (i) optimally planning longitudinal studies under constrained resources; (ii) refining or modifying hypotheses through comprehensive exploratory data analysis; (iii) appropriately modeling unequally spaced measurements, context effects, and individual differences in longitudinal research; and (iv) modeling the emergence of individuality and its relationship to brain plasticity.

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 continuous-time SEM, called ctsem. It is suited for the analysis of panel \((N > 1)\) and time series \((N = 1)\) data. By using stochastic differential equations to estimate an underlying continuous process, continuous-time models can accommodate 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. Within- and between-person effects are estimated simultaneously, and exogenous shocks of different types as well as oscillating processes can be specified.

Ongoing work is concerned with a novel class of models, Gaussian process panel models (GPPM), suitable for expressing complex hypotheses about change. This class of models draws upon ideas from Gaussian process regression, a powerful and generic nonparametric regression technique in machine learning. GPPM provides a flexible specification framework that subsumes most classic analysis approaches (e.g., SEM, Generalized Linear Models, Generalized Additive Models, or State Space Models). In his dissertation, Julian D. Karch (2016) showed that GPPM also offers novel characterizations of change that cannot be formalized within the other frameworks. Similar to ctsem, GPPM is well suited for continuous–time modeling, allowing for unequal time lags both between measurements and across people. The empirical comparison between the GPPM toolbox for Matlab and existing SEM software reveals that the GPPM representation of common longitudinal SEM may decrease computation time for param-

Key References


eter estimation by up to a factor of 9. The project members have made various further contributions to making the estimation of SEM more efficient in practice. In a related project, Karch proposed a machine-learning inspired approach to better account for interindividual differences in models relating oscillatory brain activity to behavior (Karch, Sander, von Oertzen, Brandmaier, & Werkle-Bergner, 2015).

In her dissertation project, Janne Adolf investigates the application of formal models to intense longitudinal data on daily emotion experiences and behaviors, with an emphasis on dynamic models that incorporate the changing contextual conditions of emotional experiences and behaviors. Andreas M. 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, Brandmaier, & Tsang, 2015). Ωnyx automatically generates model syntax to interface with other software packages, for example, OpenMx, lavaan, and Mplus.

Optimizing the Design of Longitudinal Studies

Longitudinal studies often require a large investment of resources and are often characterized by a relatively large number of individuals, a range of more or less reliable measurement instruments, and a relatively small number of measurement occasions. When applied to the measurement of change, the statistical power to detect a particular effect, that is, the probability that a statistical test will reject a false null hypothesis of no effect, is the primary indicator of change sensitivity and intuitively or explicitly informs the research design of longitudinal panel studies. Based on power equivalence theory (von Oertzen, 2010), von Oertzen and Brandmaier (2013) showed formally how design-related choices affect power and how these choices can be used to optimize the efficiency of longitudinal designs while keeping power constant. To evaluate change sensitivity and thereby enable researchers to generate alternative, power-equivalent study designs, Brandmaier, von Oertzen, Ghisletta, Hertzog, and Lindenberger (2015) introduced LIFESPAN, a new statistical tool that allows researchers to interactively modify and optimize longitudinal study designs (see Figure 23 for an example). In ongoing work, the group is extending this framework to arrive at an integrated understanding of measures of precision, reliability, and effect size for individual differences in change.

Brain–Behavior Relations and the Emergence of Individuality

Together with colleagues from the DFG Center for Regenerative Therapies and the German Key References


Key References


Center for Neurodegenerative Diseases (DZNE), Dresden, Andreas M. Brandmaier and Ulman Lindenberger introduced a new paradigm to better understand the contribution of development to individual differences. In the original experiment (Freund et al., 2013), the researchers observed 40 genetically identical mice that were kept in an enclosure offering a great variety of different options for exploration. The mice were equipped with tiny radio-frequency identification chips that emitted electromagnetic signals whenever they came across any of the antennas distributed throughout the cage. The researchers hypothesized that, despite their identical genetic makeup and exposure to a nominally identical environment, the mice would end up showing different behaviors and that these differences would increase over time. To quantify individual differences in exploration behavior, Andreas M. Brandmaier suggested roaming entropy (RE). RE was defined as the Shannon entropy of a spatial distribution describing the probability of finding a mouse at a particular location in the cage. Mice with low RE typically have local spatial distributions, that is, they restrict themselves to staying within certain limited areas of the enclosure. By contrast, mice with high RE make full use of the complex environment and show less preference for certain areas of the cage (see Figure 24).

The observed individual differences in behavioral trajectories were large and statistically reliable. Even more intriguingly, there was a correlation between RE and brain plasticity: Mice that explored their habitat more thoroughly also grew a greater number of new neurons in the hippocampus. Thus, with the help of advanced information-theoretic and statistical methods, including SEM, it was possible to show that personal experiences and individual behavior contribute to the individualization of the brain. In a replication study (Freund et al., 2015), we investigated to what extent mechanisms of individualization have a social component. Together with Gerd Kempermann and his team, we will continue working with this animal model to address whether and how epigenetic mechanisms contribute to the emergence of individual differences.

Exploratory Data Mining

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. Brandmaier, von Oertzen, McArdle, and Lindenberger (2013) introduced SEM Trees to provide a versatile solution to this variable selection problem. 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 (Brandmaier, Prindle, McArdle, & Lindenberger, 2016) are a recent extension of SEM trees. They are large ensembles of SEM trees, each based on a random sample of the original data. By aggregating the predictive information in a forest, one obtains 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. Brandmaier (2015) also continued to work on model-free tree structures for clustering time series. He proposed Permutation Distribution Clustering (pdc) as a novel clustering scheme that encodes dissimilarity between time series as differences in their complexity.
Figure 24. The emergence of individuality in genetically identical mice living in a nominally identical environment. (a) Shows a schematic illustration of the enclosure that housed 40 female mice. (b) Illustrates roaming entropy, which quantifies the coverage of space for a given individual. The heatmaps depict the probability of a mouse being at a specific location in the cage. Low probabilities are shown in blue, medium probabilities in green, and high probabilities in beige (see the arrow on the left). The boundaries of the cage, levels, and nesting boxes are indicated in white. The antenna positions are shown in black. The left panel shows a mouse with low roaming entropy (Animal No. 2 at day 19) and the right panel shows a mouse with high roaming entropy (Animal No. 93 at day 9). (c) Measurements of roaming entropy were aggregated into four adjacent time periods to obtain an index of cumulative roaming entropy (cRE). Each line displays the cRE for a single mouse. Corresponding levels of neurogenesis are continuously color coded from low (blue) to high (yellow). The mice differed reliably in rates of linear change in roaming entropy. (d) Individual differences in cumulative roaming entropy are associated with individual differences in adult hippocampal neurogenesis. The number of new neurons correlated significantly with cumulative roaming entropy at T4, $r = 0.46$ ($t = 3.227$, $p = 0.0026$) (adapted from Freund et al., 2013).

© MPI for Human Development


experiences across 100 days are less variable and less complex than younger adults! *Psychology and Aging, 30*, 194–208. doi:10.1037/a0038690


Infurna, F. J., Gerstorf, D., Ram, N., & Heckhausen, J. (2016). Analytic strategies for the study of adaptation to major life events: Making the most of large-scale longitudinal surveys. In H.-P. Blossfeld, J. von Maurice, M. Bayer, & J. Skopek (Eds.), Methodological issues of large-scale longitudinal surveys: The example of the National Educational Panel Study (pp. 19–35). New York: Springer. doi:10.1007/978-3-658-11994-2_2


