Exploring the Potential and Limits of Behavioral Development:
The Need for Integration Across Domains, Timescales, and Levels of Analysis

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Abstract

Important dimensions and events in human life, such as impulse control in adolescence or health and longevity in old age, vary greatly within and across people. Identifying, understanding, and possibly ameliorating both the variable and the invariant aspects of the human life course are important goals for science and society. To make progress towards these goals, researchers need to empirically and conceptually integrate evidence on developing individuals across domains of functioning, timescales, and levels of analysis. This integration requires sustained collaborative efforts across disciplines, with a particular emphasis on large-scale studies that combine experimental and longitudinal research designs. Traditional divides between the natural and the social sciences need to be overcome to facilitate a comprehensive investigation of the human life course.
Central Concepts and Requirements

Behavioral development extends from conception to old age, and includes growth and decline as well as continuity and change (Baltes, Lindenberger, & Staudinger, 2006; Li et al., 2004; Lindenberger, 2001). To provide explanations of behavioral development, the effects of agents external to the individual, such as parents’ educational aspirations, teachers’ classroom behavior, or a state’s retirement policies, need to be mapped onto mechanisms and organizational laws that operate and evolve within the developing person (e.g., Molenaar, 2008; Nesselroade, 1991).

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, correlates, and 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 (Li, 2003).

Maturation, Learning, and Senescence

To make progress in the study of behavioral development, it is helpful to distinguish among three sets of mechanisms that jointly determine behavioral development. 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, respectively. In addition, learning, at any point during ontogeny, denotes more or less durable changes in brain states induced by behavior–environment interactions (Lindenberger, Li, & Bäckman, 2006; Craik, 2006).
Maturation and learning are interdependent and nurture each other, especially early in ontogeny. For instance, neuronal circuits in the brain are shaped by experience during ‘critical periods’ in early postnatal life (Hensch, 2005). Similarly, the ways in which senescence takes its toll on the brains of aging individuals depend on individuals’ past and present learning and maturational histories. For instance, for most content domains, older adults and children vastly differ in the amount of task-relevant experience-related knowledge. It follows that older adults may be more likely to retrieve world knowledge and past memory episodes while trying to encode new information (Werkle-Bergner, Müller, Li, & Lindenberger, 2006). Perhaps most importantly, 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 (Raz et al., 2005). For instance, neurogenesis and synaptogenesis, which can be seen as expressions of maturation, continue to exist in the adult and aging brain (Kempermann, 2005), and declines in dopaminergic neuromodulation, which indicate senescence-related changes in brain chemistry, commence in early adulthood (Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006).

In sum, maturation, senescence, and learning mutually enrich and constrain each other throughout the lifespan, and they are dependent on and influenced by the properties of the physical and social environment. For instance, social institutions structure the life course in a more or less age-graded manner (Mayer, 2003), and technological and medical advances have led to a massive and continuing increase in longevity.

Life expectancy at birth is rising by about three months per year in Germany and other countries with long life expectancies, largely because of ongoing reductions in mortality after age 65 and especially after age 80 (see Table 1 and Figure 2, adapted from Christensen et al., 2009). Deaths are being postponed even at advanced ages and health is improving. The period of disability that often marks the final years of life is being pushed to higher ages commensurate with progress in lengthening the span of life. The evidence for mortality improvement is solid, but, in part because it is easier to
measure mortality than health and in part because of the lack of large longitudinal studies, evidence for improvement in physical performance at older ages is somewhat mixed, and evidence for improvement in cognitive performance at age 80, say, or age 90, is weak. Put differently, the mechanisms through which social changes impinge upon and are influenced by behavioral change are difficult to assess. For instance, individual differences in cognition, health, and longevity are associated with income and other aspects of socioeconomic status, but the causal pathways underlying this association are only partially understood.

Behavioral and Neuronal Plasticity

Behavioral plasticity (also see Villringer, MPG 2010 Plus; Mercado, 2008), or the alteration of developmental trajectories through experience, is a precious phenomenon (Hertzog, Kramer, Wilson, & Lindenberger, 2009). Inquiries into the plasticity of human 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, cognitive intervention 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, or neurofunctional imaging measures are assessed before, during, and after training, intervention studies also offer new insights into relations between behavioral and neuronal levels of plasticity (Lövdén et al., 2010). Thus, by partly taking control over behavior–environment interactions, the mechanisms of learning can be studied in the context of maturation and senescence. When longitudinal information is available, intervention studies bridge the gap between short-term alterations in performance and long-term developmental trajectories (e.g. Singer, Lindenberger, & Baltes, 2003).
From the larger perspective of societal evolution, intervention studies help to explore the range of possible development, or what could be possible in principle if conditions were different (see Figure 3, from Hertzog et al., 2009). Comparisons of countries and historical studies of change over time also can be informative (see Figure 3, adapted from in Christensen et al., 2009). The resulting 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 human development.

Domains, Timescales, and Levels of Analysis: The Need for Integration

If lifespan changes in behavior are conceived as recursive interactions among maturation, learning, and senescence, then three difficult integrative tasks emerge. First, there is the need to integrate theorizing and research practice across functional domains to attain a comprehensive picture of individual behavioral development, including its variable and invariant properties. Ever too often, different domains such as sensation, perception, motor performance as well as various aspects of cognition, volition, and motivation are studied in isolation, even though their functioning and evolution is highly interdependent and can only be understood if studied together.

Second, there is a need to discriminate between processes operating at different timescales, and to understand the mechanisms that link short-term variations to long-term change (S.-C. Li, Huxhold, & Schmiedek, 2004; Lindenberger & von Oertzen, 2006; Ram, Lindenberger, & Blanchard-Fields, in press). 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 act as short-term precursors of long-term development, driving development into more or less beneficial directions.

Third, to arrive at mechanistic explanations of behavioral change, there is the need to connect behavioral, neuronal, and genetic levels of analysis. The phenotype, or
the observable behavior of individuals, needs to be related to the their endophenotype, or internal organization, and the ways in which this internal organization is genetically regulated. Accumulating evidence indicates that 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 intended behavior (Pascual-Leone et al., 2006). Therefore, ontogenetic changes in behavioral repertoires are likely to be associated with more or less continuous changes in multiple brain–behavior mappings. Some of these re-mapping 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 the three.

The Benefits of Integration: Examples

The preceding considerations suggest that the study of behavioral change is facilitated by research that meets one or more of the following three criteria: (a) focus on developing individuals in the context of their physical and social environments; (b) explore and track individuals' plasticity; and (c) collect and conceptually integrate evidence across domains of functioning, timescales, and levels of analysis. While these three criteria may seem uncontroversial, their implications for research design and collaboration are often neglected in scientific practice, which tends to be restricted to specific content domains, timescales, and levels of analysis. In the following, we will first provide examples for lines of research that fulfill some but not all of these three criteria. Then, we will propose that future research should rely more heavily on research designs that simultaneously most or all.

Focusing on the Individual: Exploring Within-person Structures

Most existing research on individual traits assumes that covariance structures based on between-person differences generalize to within-person structures. However,
as Raymond B. Cattell (1952), Jacques Lautrey (2003), John Nesselroade (1991), Peter Molenaar (2008), and others have argued for a long time, differences between intra-person and inter-person structures are not only possible but even likely, given the malleability of brain and behavior and the diversity of developmental trajectories (Li & Lindenberger, 2002; Li, 2003).

In an initial attempt to address this issue, Brose et al. (in press) observed measures of motivation and cognitive performance (i.e., working memory) in 101 younger and 103 older adults across 100 daily occasions. In younger adults, correlations between motivation and WM were generally positive in the sense that many younger adults tended to perform better on days at which they also reported to be more motivated. In older adults, motivation was less variable and less strongly related to cognitive performance. Most importantly, within-person structures differed reliably across individuals, defying the notion that between-person structures are a proxy for within-person associations (see Figure 4). These findings stress the need to carefully study within-person structures, including their dynamic properties and age-related changes.

Exploring Cognitive Plasticity: Acquisition of Skilled Episodic Memory Performance

Episodic memory denotes the conscious remembrance of events, happenings, and situations relating the past, present, and future (Tulving, 2002). Remembering past events is a universal human experience that starts relatively early in life. Researchers in the fields of cognitive development and cognitive aging have been working on understanding how memory develops and changes within confined age periods (for reviews, see Kausler, 1994; Schneider and Pressley, 1997). However, little effort has been invested in directly examining age differences in memory plasticity and integrating the mechanisms underlying memory changes across the lifespan (Craik & Bialystok, 2006; Shing & Lindenberger, submitted).

A study by Brehmer, Li, Mueller, von Oertzen, and Lindenberger (2007) is one of the few studies that directly compared memory plasticity from middle childhood to
early old age. The authors used a multi-phase training design consisting of baseline assessment, strategy instruction, and strategy practice to compare the plasticity of episodic memory performance in younger children aged 9-10, older children aged 11-12, younger adults aged 20-25, and older adults aged 65-78. The participants learned and practiced the Method of Loci, an imagery-based mnemonic technique, to encode and retrieve words by location cues. Children performed at similar levels as older adults at baseline and after being instructed in the strategy (see Figure 5). However, children profited considerably more than older adults from subsequent practice in the strategy, leading to a magnification of age differences between children and older adults in the course of the experiment.

In a follow-up study with the same sample, Brehmer et al. (2008) examined the long-term maintenance of the use of the mnemonic strategy 11-months after the original training study had been completed. Maintenance performance was tested in two sessions, the first without and the second with mnemonic re-instruction, to assess both spontaneous and reactive maintenance of skill. Children in both age groups spontaneously showed performance improvements beyond the level that they had attained 11 months earlier, and did not gain any further from renewed instruction in the second follow-up session. In contrast, older adults showed a decreasing trend in performance after 11 months, and then improved reliably from the first to the second retest session. Taken together, these results suggest that developmental plasticity in middle childhood reflects a powerful alliance between learning and maturation that permits enhancement of skilled episodic memory performance without the need for re-instruction.

Linking Functional Domains: Adult Age Differences Changes in the Relation Between Sensorimotor and Cognitive Functioning

Everyday life often requires the integration of multiple sensory inputs and concurrent coordination of sensorimotor and cognitive demands. Examples are walking while trying to memorize a shopping list, maintaining one's balance on a bus while
trying to read an advertisement, or trying to remember the way to a friend’s house while driving in the hectic morning traffic. Age-comparative studies suggest that interdependencies between sensorimotor and cognitive tasks or task demands increase from early to late adulthood. Using a virtual reality projected in front of a treadmill, Lövdén et al. (2005) asked younger and older adults to find and remember the way to the bistro in museums under conditions of walking with support (holding on to a handrail) or without support until they reached perfect performance. Walking support attenuated age-related decrements in navigational learning (see Figure 6), and walking with navigation load increased older adults’, but not younger adults’, trunk-angle variability. Thus, walking demands influenced the navigation performance of older, but not younger adults. Apparently, sensorimotor aspects of behavior are more attention-demanding in older adults than in younger adults, and attentional resources are reduced. These two tendencies lead to increased competition between sensorimotor and cognitive tasks or task components for scarce attentional resources (Schaefer, Huxhold, & Lindenberger, 2006). Modern technology can help to attenuate the adverse effects of this quandary (Lindenberger, Lövdén, Schellenbach, Li, & Krüger, 2008).

Linking Timescales: Short-term Fluctuations Predicting Long-term Change

It has been suggested that aging systems show an increase in moment-to-moment fluctuations at both behavioral and neuronal levels, reflecting decrements in the efficiency of regulatory mechanisms. According to this hypothesis, older individuals with greater moment-to-moment fluctuations at a given time should be more likely to experience cognitive decline. In a study combining the observation of short-term variability with the tracking of long-term change, Lövdén et al. (2007) applied structural equation modeling to 13-year longitudinal data from the Berlin Aging Study to test this prediction. Trial-to-trial reaction time variability in perceptual speed preceded and predicted greater cognitive decline in perceptual speed and ideational fluency (see Figure 7). This finding suggests that trial-to-trial variability signals impending decline in
cognitive performance, and that theories of neurocognitive aging need to postulate developmental cascades between senescent changes in variability and central tendency.

Linking Timescales: Secular Changes in Longevity

Most children born since the year 2000 in developed countries probably will celebrate their 100\textsuperscript{th} birthdays—in the 22\textsuperscript{nd} century. In Germany and similar countries, however, life expectancy today is about 80, two decades short of 100, and life expectancy a century ago was roughly 50. Because of health, economic and social change, different birth cohorts are experiencing different life courses, and are experiencing secular changes at different ages. In 2010, for instance, people born in 2000, 1970 and 1940 will be 10, 40 and 70 years old. Understanding the human life course requires linking the lives of birth cohorts to secular changes over time. It is crucial to longitudinally study not just people born around year \textit{Y}, but also people born around year \textit{Y}-10 and year \textit{Y}+10 and, if feasible, more distant birth years as well.

Linking Levels of Analysis: Adult Age Modulates the Effects of Genetic Differences on Cognition

Cognitive aging is a heterogeneous phenomenon: Older adults who preserve high levels of cognitive functioning into very old age stand in sharp contrast to age-mates whose cognitive resources are waning by the time they reach later adulthood (Bäckman et al., 1999). Longitudinal studies confirm that individual differences in cognitive performance increase from early to late adulthood (e.g., de Frias et al., 2007), and suggest that both genetic and environmental factors contribute (Finkel et al., 2005). This increasing cognitive heterogeneity in aging likely stems from a multitude of factors, an obvious category being disease (e.g., the presence or absence of dementia and old-age depression).

Advances in molecular genetics render it possible to identify specific genes affecting brain chemistry, structure, and function, as well as associated cognitive functions in humans (Goldberg and Weinberger, 2004). At present, close to 100
candidate genes influencing human brain functions and cognition have been reported (e.g., de Geus et al., 2008; Payton, 2009). Any given gene is likely to affect more than one cognitive function, and variations in any given cognitive function are likely to be influenced by more than one gene. For example, the brain circuitries implementing working memory and episodic memory show considerable overlap, and the proteins coded by different genes are generally active in more than one brain region. Therefore, recent publications stress the need to consider gene-gene interactions (de Geus et al., 2008; Kovas and Plomin, 2006). Despite (or perhaps because of) these complications, the identification of cognitively relevant genes carries the promise to refine and constrain our knowledge about neurobiological mechanisms in human cognition, including its age-graded changes, especially if the physiological effects of the gene are reasonably well understood.

Recently, Lindenberger et al. (2008) hypothesized that losses in neurochemical and anatomical brain resources in normal aging modulate the effects of common genetic variations on cognitive functioning. This hypothesis is based on the assumption that the function relating brain resources to cognition is nonlinear, so that genetic differences exert increasingly large effects on cognition as resources recede from high to medium levels in the course of aging (see Figure 8). Two recent studies provide direct empirical support for this hypothesis. First, Nagel et al. (2008) found that the effects of the Catechol-O-Methyltransferase (COMT) gene, on cognitive performance are magnified in old age and modulated by the brain-derived neurotrophic factor (BDNF) gene. The COMT gene affects enzymatic activity resulting in the degradation of dopamine in prefrontal cortex, whereas the BDNF gene affects the BDNF protein, which enhances long-term potentiation and associative binding in the medial-temporal lobes. Second, Li et al. (in press) compared the influence of the BDNF gene on serial order memory in younger and older healthy adults. The authors found a BDNF effect for backward recall in older adults only, with any Met carriers (i.e., individuals with reduced BDNF signaling) recalling less accurately than Val homozygotes (see Figure 9).
Linking Levels of Analysis: Delineating the Relations Among Level of Task Performance, Brain Activation, and Age

Working memory, or the process of holding information “on-line” to perform tasks in the absence of external cues is compromised in old age (Babcock & Salthouse, 1990). Individual differences in WM performance are large and increase with age. The neural network typically activated during spatial WM tasks involves lateral prefrontal cortex, premotor cortex, posterior parietal cortex, and temporal brain regions (D’Esposito et al., 1998). FMRI studies reveal that decreased WM performance in older adults is paralleled by age-related changes in functional brain activation patterns (Reuter-Lorenz et al., 2000).

In younger adults, activation of the WM network is affected by memory load. The load-dependent change of the BOLD signal can be characterized as a dose-response function. Interestingly, the shape of dose-response functions differs among studies. Some researchers have reported monotonically increasing functions that are either linear (Braver et al., 1997) or nonlinear (Cohen et al., 1997). Others have found inverted U-shaped functions, where activation in dorsolateral prefrontal cortex increases with load up to a certain difficulty level, and then decreases (Callicott et al., 1999).

Evidence based primarily on episodic memory studies suggests that brain activation patterns can be modulated by task difficulty in both younger and older adults. In most fMRI aging studies on WM, however, performance level has not been considered, so that age differences in activation patterns are confounded with age differences in performance level. Recently, Nagel et al. (in press) addressed this issue by comparing younger and older low and high performers in an event-related fMRI study. Thirty younger (20-30 years) and 30 older (60-70 years) healthy adults were tested with a spatial WM task with three load levels. In both age groups, a region-of-interest analysis revealed marked differences in the activation patterns between high and low performers in both age groups. Critically, among the older adults, a more “youth-like” load-dependent modulation of the BOLD signal was associated with higher levels of
spatial WM performance. In the meantime, this finding has been replicated and extended to verbal working memory (Nagel et al., in press).

Large-Scale Investigations of the Human Life Course:
A List of Criteria and a Plea for Collaboration

The general considerations and research examples outlined in this article underscore the benefits of an integrated, multidisciplinary approach to the study of the human life course. In sum, this amounts to a plea for large-scale panel studies that bridge the gap between the natural and the social sciences, and that combine experimental intervention with longitudinal observation to chart the potential and identify the mechanisms of individual development (see Figures 1–3).

Some critical design features of such studies are listed below. Clearly, it is unlikely that any given empirical investigation will include all of these characteristics. However, the more of these features are included, the more likely will it be that a given study produces palpable advances in our knowledge about the mechanisms, the diversity, and the malleability of behavioral development across the lifespan.

The key design features are the following:

(1) The sampling units are households rather than individuals. One of several advantages of a household design relative to a person-based design is that children can be recruited into the study before birth to assess pre- and perinatal influences on development as well as the factors influencing the likelihood of child bearing (Gert Wagner, personal communication, April 2008). Another advantage is better access to and a more complete assessment of each individual’s immediate social and physical environment.

(2) The sample of households is sufficiently large and heterogeneous to permit intervention studies with random or yoked assignment to control and experimental groups within stratified subgroups (e.g., by age, sex, or risk status
in relation to a developmental outcome of interest). This enables researchers to longitudinally evaluate intervention effects in different groups.

(3) The study oversamples identical and fraternal twins and other sibling relations to facilitate the combined use of behavior genetics and molecular genetics in understanding the effects of and the interaction between genetic and environmental sources of variation on individual differences in behavioral development.

(4) The study oversamples very old people to study the antecedents, correlates, and consequences of longer lives and of population aging.

(5) The assessment protocol of the study includes psychological, biological, sociological, and economic assessments of sufficient density to delineate short-term variation and long-term development at the individual level.

(6) Using state-of-the-art technology, the assessment protocol includes a close description of the physical and social environment, which often has been neglected in past work (cf. Dhami, Hertwig, & Hoffrage, 2004).

(7) The study follows several different birth cohorts to permit the analysis of secular changes, such as in cognitive functioning, that are associated with longer, healthier lives, more education, greater income and other factors that are changing over historical time.

(8) The study is part of a concerted effort that includes at least three or four different countries to identify mechanisms and trends that generalize across cultures as well as country-specific cultural differences, which may help to discover mechanisms that otherwise would go unnoticed.

It is worth noting that existing longitudinal studies are expanding their research designs along one or more of criteria listed above. For instance, the BETULA study, a longitudinal multiple-cohort study with an emphasis on adult cognitive development and aging, has added neuronal assessment to its measurement protocol (Persson et al., 2006). Similarly, large-scale sociological and economic longitudinal panel studies, such as the German Socioeconomic Panel Study (SOEP; Wagner et al., 2007) and the British
Household Panel Study (Taylor et al., 2008), which both are based on households as sampling units, keep adding psychological and biological variables to their protocol. In each of these studies and the disciplines that triggered them initially, the awareness is growing that a better understanding of the human life course requires sustained collaborative efforts across disciplines.

With its large spectrum of disciplines and its long-term funding scheme, the Max Planck Society is particularly well equipped to combine experimental and longitudinal research designs in the context of large-scale studies on the human life course. Several graduate programs, such as the International Max Planck Research School (IMPRS) Demography, the MaxNetAging Research School, and the IMPRS on the Life Course provide training opportunities for researchers early in their careers who share an interest in lifespan development. In addition, the Max Planck Research Network on Cognition (Maxnet Cognition) provides a forum for fostering collaboration across institutes and for coordinating research activities with research consortia outside the Max Planck Society. The infrastructure for collaborative research efforts has been established, and the planning and implementation of the kind of studies envisioned in this article is within reach.
References


Vaupel

Table 1. *Age-specific contributions to the increase in record life expectancy in women from 1850 to 2007.* From Christensen, Dobblhammer, Rau, and Vaupel (2009).

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<td>0-14 years</td>
<td>62.13%</td>
<td>54.75%</td>
<td>30.99%</td>
<td>29.72%</td>
<td>11.20%</td>
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<td>15-49 years</td>
<td>29.09%</td>
<td>31.55%</td>
<td>37.64%</td>
<td>17.70%</td>
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<td>50-64 years</td>
<td>5.34%</td>
<td>9.32%</td>
<td>18.67%</td>
<td>16.27%</td>
<td>24.29%</td>
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<tr>
<td>65-79 years</td>
<td>3.17%</td>
<td>4.44%</td>
<td>12.72%</td>
<td>28.24%</td>
<td>40.57%</td>
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<td>&gt;80 years</td>
<td>0.27%</td>
<td>-0.05%</td>
<td>-0.03%</td>
<td>8.07%</td>
<td>17.47%</td>
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Figure Captions

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

Figure 2 *Best-practice life expectancy and life expectancy for women in selected countries from 1840 to 2007.* The linear regression trend is depicted by a solid grey line with a slope of 0.24 per year. From Christensen, Dobhlammer, Rau, and Vaupel (2009).

Figure 3 *Hypothetical illustration of the zone of possible cognitive development for a given individual, along with four developmental curves indicating specific possible outcomes.* Inquiries into the modifiability (plasticity) of human 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. Adapted from Hertzog, Kramer, Wilson, & Lindenberger, 2009).

Figure 4 *Distributions of the latent correlations between motivation and cognitive performance in younger and older adults.* Correlations are either based on differences between persons at a given point in time (between-person correlation), or on differences between days for a given person (within-person correlation). In both age groups, the range and the mean of between-person and within-person correlations differ considerably. Hence,
between-person structures relating motivation to cognitive performance do not provide a good approximation to within-person structures. Adapted from Brose et al. (2010).

Figure 5  
*Plasticity of episodic memory performance from middle childhood to old age.*
Age differences before instruction, after initial instruction, and after multi-session practice and training. Post-instruction scores for younger adults cannot be interpreted because of ceiling effects; all other data points are interpretable. Children profited considerably more than older adults from subsequent practice, leading to a magnification of age differences between children and older adults in the course of the experiment. Adapted from Brehmer et al. (2007).

Figure 6  
*Adult age differences in way-finding (spatial navigation) performance are shaped by sensorimotor demands.* Bars display the mean distance covered to criterion as a function of age group (young and older adults) and walking demand (with or without handrail support). Provision of a handrail does not alter the way-finding performance of the younger adults, but considerably improves the way-finding performance of the older adults. Adapted from Lövdén et al. (2005).

Figure 7  
*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. Recent empirical evidence supports this prediction. Adapted from Lövdén et al. (2007).
Figure 8  *The resource modulation hypothesis posits that losses in chemical and structural brain resources associated with normal aging modulate the effects of common genetic variation on cognitive performance.* As normal aging moves individuals’ resources from the top to the middle portion of the resource function, constant amounts of genetic variation are translated into increasingly larger performance differences. With depleted resources, genetic effects are expected to dwindle again. The colored circles represent eight individuals with different combinations of genetic polymorphisms as they move from early adulthood over old age to dementia or terminal decline. Adapted from Lindenberger et al. (2008).

Figure 9  *Proportion of words recalled in correct serial position as a function of age group, BDNF genotype, and portion of the curve in backward serial recall.* Error bars represent standard errors around the means. The effect of BDNF genotype is found in older adults only, with Met-allele carriers (i.e., individuals with reduced BDNF signaling) recalling fewer items than Val homozygotes. The effect is also specific to the primacy and middle portions of the serial-position curve, where intra-list interference and associative demands are especially high. Adapted from Li et al. (in press).

Figure 10  *Performance level modulates adult age differences in patterns of working-memory related brain activation.* Region-of-interest analysis for the extreme groups. BOLD signal changes in high- and low-performing younger and older adults across load (younger adults: blue; older adults: red; lower task demand is represented by lighter colors). * p < .05; + = .05 < p < .10; L = linear contrast; Q = quadratic contrast. There are marked differences in BOLD response between high and low performers within and across age groups, as indicated by reliable age by performance by load interactions in 4 of the 6 regions of interest. Adapted from Nagel et al. (in press).
Figure 1
Figure 3
Figure 4

2-Factor Model: Motivation and Performance

Between-person Analyses

- Younger Adults
  \[ M = -0.27 \]
  \[ (0.10) \]

- Older Adults
  \[ M = -0.06 \]
  \[ (0.07) \]

Within-person Analyses

- Younger Adults
  \[ M = 0.43 \]
  \[ (0.34) \]

- Older Adults
  \[ M = -0.21 \]
  \[ (0.27) \]
Figure 5
Figure 6
Figure 7
Figure 9
Figure 10

A. Left DLPFC

B. Left PMC

C. Left PPC

Right DLPFC

Right PMC

Right PPC

Young
- Load 1
- Load 2
- Load 3
- Load 7

Old
- Load 1
- Load 3
- Load 7

% Signal Change

Young High Young Low Old High Old Low

Young High Young Low Old High Old Low

Young High Young Low Old High Old Low