

Editorial

Delineating brain–behavior mappings across the lifespan: Substantive and methodological advances in developmental neuroscience

Throughout the lifespan, the changing brain and the changing physical and cultural environment shape behavior. At the same time, behavior alters both the brain and the environment. Hence, environment and brain act as antecedents, but also as consequents of both moment-to-moment variability and long-term change in patterns of behavior (e.g., [Baltes et al., 2006](#); [Li and Lindenberger, 2002](#); [Nesselroade, 1991](#)).

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 (see [Fig. 1](#); cf. [Li and Lindenberger, 2002](#)). In attempts to explain the development of this system during ontogeny, maturation and senescence denote the operation of age-graded brain mechanisms at neurochemical, neuroanatomical, and functional levels of analysis 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 depends on individuals' past and present learning and maturational histories. Also, to further complicate matters, processes commonly associated with maturation are not confined to early ontogeny, and processes related to senescence are also not restricted to old and very old age. For instance, neurogenesis and synaptogenesis, as expressions of maturation, continue to exist in the adult and aging brain (see [Kempermann et al., 2004](#), for review), and declines in dopaminergic neuromodulation, which indicate senescence-related changes in brain chemistry, commence in early adulthood. Thus, maturation, learning, and senescence mutually enrich and constrain each other throughout the lifespan, and must be studied as interacting forces driving the brain–behavior–environment system.

Studying these interactions is a challenging but rewarding task, as the relations, or “mappings”, between brain states and behavioral states change throughout ontogeny.

Take, for instance, the mechanisms by which children and older adults encode new biographic episodes (cf. [Werkle-Bergner et al., 2006](#)). Due to their learning histories, older adults possess more task-relevant knowledge than children for most domains of life. Therefore, older adults are more likely to retrieve world knowledge and past experiences while processing new information than children. Hence, integration of new information into existing bodies of knowledge during encoding may be more predictive for learning success in older adults than in children.

It follows that the brain machinery that drives the encoding, storage, and retrieval of new episodes likely differs profoundly between children and older adults, even when the average levels of performance observed in these two groups, as assessed by the number of correctly remembered episodes, do not differ. For instance, prefrontal cortex activity may be more strongly related to successful encoding in older adults than in children because retrieval processes during encoding (e.g., [Tulving, 1967](#)), which may be of greater functional relevance for older adults, involve prefrontal areas ([Cabeza and Nyberg, 2000](#)). At the same time, prefrontal areas of the neocortex are among the last to mature during childhood, and among the first to show signs of senescence-related deterioration during adulthood ([Raz, 2000](#); [Raz et al., 2005](#)). Thus, interindividual differences in maturation may be linked to prefrontal involvement in successful encoding among children, and increased reliance on past knowledge among older adults may be compromised by deficient prefrontal circuitry. As this example demonstrates, lifespan changes in brain mechanisms, such as those supporting the encoding of new episodes, are shaped by complex interactions among processes related to maturation, learning, and senescence.

Furthermore, at any given point in ontogenetic time, one-to-one mappings between brain states and behaviors are probably the exception, rather than the rule, as the brain generally offers more than one implementation of an adaptive behavioral outcome ([Baltes and Baltes, 1990](#); [Edelman, 1987](#); [Lautrey, 2003](#); [Li, 2003](#); [Pascual-Leone et al., 2005](#)). Therefore, changes in behavioral repertoires are accompanied by continuous changes in multiple

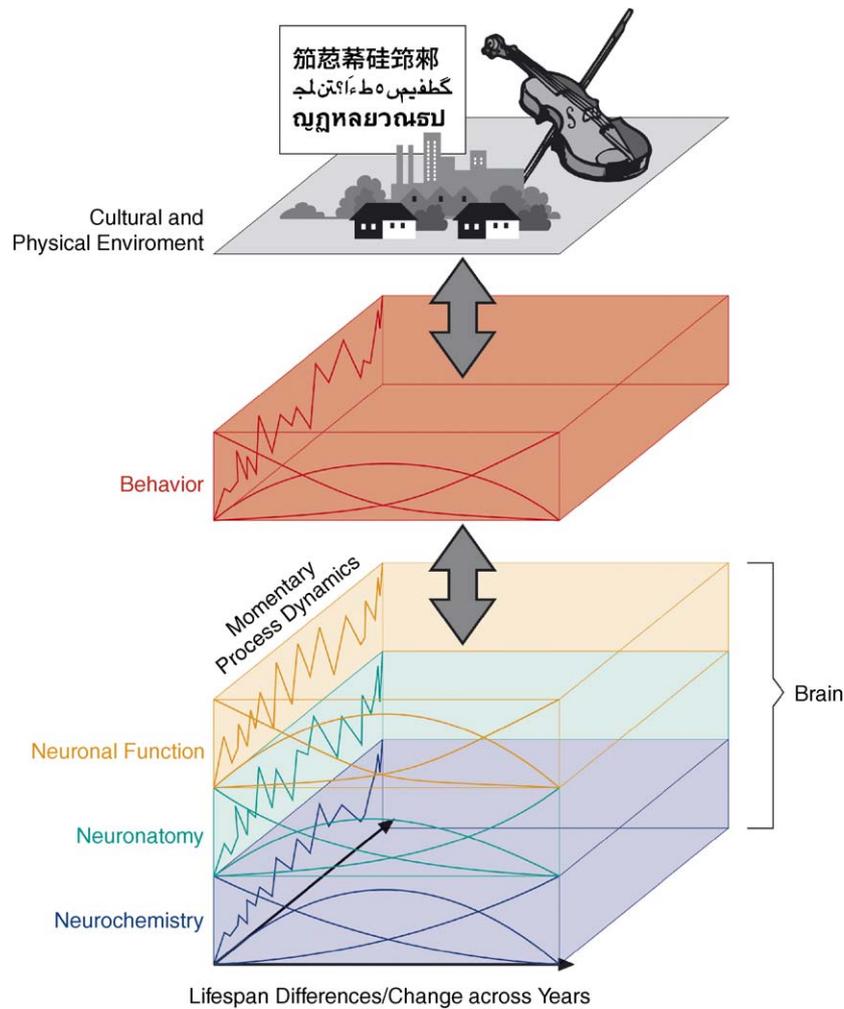


Fig. 1. Environment and brain act as antecedents and consequents of moment-to-moment variability and long-term changes in patterns of behavior. Lifespan changes in brain–behavior mappings are shaped by complex interactions among processes related to maturation, learning, and senescence. The identification of key players in the ontogeny of brain–behavior dynamics across the lifespan 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. See also Baltes et al., 2006; Li and Lindenberger, 2002; Lindenberger and von Oertzen, 2006.

brain–behavior mappings. Some of these re-mapping gradients may be relatively universal and age-graded, reflecting the operation of general mechanisms of maturation or senescence (e.g., expansion of white-matter tracts in childhood and adolescence; loss of dopamine receptors in adulthood), whereas others may be more variable, reflecting genetic background, person-specific learning histories, the path-dependent nature of developmental dynamics (e.g., Molenaar et al., 1993), or a combination of the three. The resulting picture underscores the diversity and malleability of the organization of brain and behavior, on the one hand, as well as constraints on diversity and malleability brought about by universal age-graded mechanisms associated with maturation and senescence, by general laws of neuronal and behavioral organization, and by cultural and physical regularities in the environment.

The bounded malleability of brain–behavior mappings in the course of ontogeny poses an enormous conceptual and methodological challenge for developmental neu-

rosience. The complexity of brain–behavior–environment dynamics, its recursions and path dependencies, often defies experimental control so that experimentation needs to be supplemented by less tightly controlled empirical approaches such as quasi-experiments and correlational techniques. However, facing these difficulties is worth the effort, as the scientific promise in studying the ontogeny of mind and brain is truly outstanding. Progress in delineating key mechanisms of age-graded changes in brain–behavior mappings will advance not only our knowledge about ontogenetic change, but also our general understanding of the dynamic interplay among brain, behavior, and environment. Prominent examples from all fields of science show that complex systems are more likely to be understood if observed during periods of emergence, re-organization, or decay, rather than during periods of relative stability.

In this context, studying the links between short-term variability and long-term change appears to be a particularly

informative research strategy for delineating key mechanisms of development (e.g., Nesselroade, 1991). For instance, aging cognitive systems show an increase in maladaptive moment-to-moment fluctuations, or decrease in processing robustness, at both behavioral and neuronal levels of analysis (Li et al., 2001, 2004; Lindenberger and von Oertzen, 2006; MacDonald et al., 2006). Neurocomputational theory (e.g., Li et al., 2001, 2006) and recent direct empirical evidence (Bellgrove et al., 2004; MacDonald et al., 2006) suggest that this increase in moment-to-moment fluctuations reflects alterations in neuronal signaling leading to greater prominence of background noise and less distinctive processing pathways and representations. Based on this premise, one would predict that aging individuals with greater moment-to-moment process fluctuations would show greater decline in mean levels of functioning across time than individuals with less such fluctuation (see Fig. 2). Recent evidence supports this prediction (MacDonald et al., 2003; Shipley et al., 2006). Conversely, and as argued by Siegler and others (e.g., Siegler, 2006), other forms of moment-to-moment variability indicate the ability to bring a wide variety of different strategies to the task, and are positively related to long-term change in both childhood (Siegler, 1994) and old age (Allaire and Marsiske, 2005). Thus, moment-to-moment variability helps direct our attention toward the identification of mechanisms underlying ontogenetic change in both negative and positive directions.

The identification of key players in the ontogeny of brain–behavior dynamics across the lifespan 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. This special issue focuses primarily on the latter; for recent summaries on advances in methodological and

computational modeling specific to child developmental neuroscience, see recent special issues/sections in *Developmental Science* edited by Casey and de Hann (2002), Spencer and Thelen (2003), and Schlesinger and Parisi (2004). The primary goal we set ourselves for this special issue was to provide an overview of substantive and methodological advances in the empirical study of lifespan changes in brain–behavior mappings. Thus, all contributions to this special issue review and discuss the ways in which methodological innovations have helped, or will help, to improve our substantive understanding of ontogenetic changes in brain structure and function and their links to behavioral development across the human lifespan.

We feel greatly indebted to all contributors to this volume who were willing to take on the difficult tasks set by the agenda for this special issue. Their contributions were classified into four broad categories: (a) neurochemistry (Li et al., 2006; Bäckman et al., 2006); (b) neuroanatomy (Lenroot and Giedd, 2006; Wozniak and Lim, 2006; Raz and Rodrigue, 2006; Sullivan and Pfefferbaum, 2006); (c) functional dynamics (Onton et al., 2006; Ritter and Villringer, 2006); and (d) exemplary illustrations of brain–behavior changes in three different behavioral domains, empathy (Singer, 2006), episodic memory (Jones et al., 2006; Werkle-Bergner et al., 2006), and reading (Laubrock et al., 2006). Each section contains contributions that cover either end of the lifespan, and some contributions cover both. Within sections, contributions were ordered by lifespan emphasis, proceeding from childhood to old age. The intrauterine and infant periods of ontogeny were not addressed in this special issue. We agree with others (e.g., Karmiloff-Smith, 1995) that neurobehavioral research on these age periods has made rapid progress in recent years, and has led to fascinating insights into the early competencies of infants and their

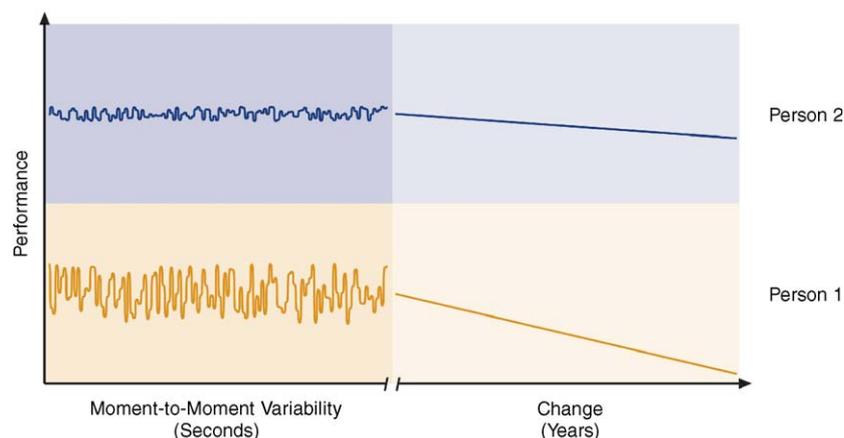


Fig. 2. Example for predictions linking moment-to-moment variability to long-term change, and brain changes to behavioral changes (cf. Lindenberger and von Oertzen, 2006; MacDonald et al., 2006). Senescent-related changes in neuromodulation lead to greater moment-to-moment fluctuation in neural signaling, thereby enhancing the prominence of background noise, reducing the distinctiveness of processing pathways and representations, and increasing variability of cognitive performance (Li et al., 2001, 2006). Hence, 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 (MacDonald et al., 2003; Shipley et al., 2006; for review, see MacDonald et al., 2006).

likely neuronal correlates. At the same time, the empirical methods used to study early ontogeny are often markedly different from those used for later periods of life, which makes it even more difficult to compare and integrate the available evidence across age periods. Thus, we decided to reduce complexity by restricting the scope of lifespan coverage to the time beyond early childhood.

Our insistence on assembling evidence from both childhood and old age was motivated by the hope that the comparative and integrative discussion of changes in brain and behavior during different periods of ontogeny, and especially during childhood and old age, will help researchers to identify the specific characteristics of each of the phases, on the one hand, and to discover general features of brain–behavior reorganization, on the other. Here, our special gratitude goes to Fergus Craik (this volume), who was willing to discuss all the other contributions and their interrelations in his closing comments. We have the impression that his commentary documents, more than each of the individual contributions viewed in isolation, that a neuroscience of behavioral development across the lifespan is indeed in the making.

Finally, we would like to thank Dr. Ann E. Kelley and Dr. Linda Porrino, past and current editors of *Neuroscience and Biobehavioral Reviews*, who welcomed our initial exposé for this special issue, as well as Ms. Sara Purdy and Ms. Sumika Sakkanishi, who assisted us during later stages of production.

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