

The Aging Mind and Brain: Implications of Enduring Plasticity for Behavioral and Cultural Change

Patricia A. Reuter-Lorenz and Joseph A. Mikels

ABSTRACT

Although aging is broadly characterized by decline, the potential for new learning and plasticity persists well into the later decades of life. Scientific advances are yielding a deeper understanding of the limitations that biological aging imposes on cognitive function, as well as new insights into how the human mind and brain respond adaptively to the aging process. Neurocognitive investigations of the reciprocity between mind and brain reveal new avenues to influence and shape neural processes that underlie mental fitness, especially in the golden years. We explore these ideas to illustrate the co-constructivist framework in operation across neural, cognitive, behavioral, and cultural dimensions as they influence late-life development.

OVERVIEW

The persistence of behavioral adaptation and plasticity (i.e., modifiability) in later life has been recognized by the field of cognitive aging for several decades (e.g., Baltes, 1997). Training procedures of various sorts have been shown to enhance cognitive performance and produce long-term gains, even for older adults well into their seventies (e.g., Willis & Nesselroade, 1990). With the recent advances in genetics, in the basic neurosciences, and in brain imaging technologies, the scope and potential of age-related reorganizational processes have attained a new level of analysis and persuasion, especially for researchers whose theoretical orientation is closely linked to brain correlates of plasticity (Park, Polk, Mikels, Taylor, & Marshuetz, 2001; Reuter-Lorenz, 2002). As documented in other contributions to this volume, and in this chapter, adult neurogenesis, cognitive improvement with physical exercise, and compensatory brain activity patterns are but a few of the more recent additional indications that

behavioral and biological plasticity, even in the golden years, is a fact of life. Indeed, identifying the sources, mechanisms, and limitations of later-life plasticity, whether they are due to nature (i.e., genetics), nurture, or both, is an endeavor of great practical and intellectual interest and, in many respects, forms the bedrock of a biocultural co-constructivist agenda for aging research.

Biocultural co-constructivism recognizes that individual lifespan development is the result of the co-constructive influences of biology and culture (i.e., experience and environment). However, co-constructivism takes the nature–nurture inquiry several steps further by examining the recursive influences of the individual on his or her own biology, of biology on the environment, and vice versa. For example, in the context of developmental changes over the lifespan, we can inquire about how the individual system adapts, both behaviorally and neurophysiologically, to its own reorganization. Moreover, one can investigate whether and how the reorganized system alters its environment and, in turn, brings new influences on itself. Understanding this kind of recursion at different levels of analysis is at the heart of the co-constructive endeavor and is one of the greatest and most novel challenges it poses.

No forum could be more appropriate than the present one to attempt to take on this challenge as it pertains to aging. We do so from a perspective framed by a novel theory that has grown out of our own research on age-related alterations in working memory and their neural underpinnings. We refer to this view as the *compensation-related utilization of neural circuits hypothesis* (or CRUNCH). This hypothesis recognizes that the aging brain adapts to its own decline by recruiting additional neural circuits not typically engaged by younger brains to optimize information processing. Such forms of compensation may have a cost in that more neural resources must be expended by an older brain to accomplish computational goals that can be completed more efficiently (i.e., with fewer circuits) by younger brains. Nevertheless, we are beginning to understand the processes of compensation and adaptation from a biological perspective, and this understanding can permit a more complete analysis of the co-constructive influences on the later stages of life.

Although this chapter focuses on an individual brain-oriented approach, we draw attention to the fact that the notion of compensation is also a cultural construct. For some cultural anthropologists (Gehlen, 1988), culture is inherently a system of compensations, usually inventions and resources that “compensate” for the shortcomings of the biological make-up of humans. Thus, although it is not the primary focus of this chapter, we want to acknowledge the view that compensatory forces are also part of the environment and through experience can shape the brain in directions similar to the brain-based account of CRUNCH (see, e.g., Baltes, 1997; Chapter 14).

As background, we begin with a basic but broad-stroke review of what is known about the declines that normally accompany neural and cognitive aging, followed by an overview of evidence indicating the extent to which plasticity endures in older age (see Chapters 2 and 11). By way of introduction to our own neurocognitive hypothesis, we discuss two related macro-level theories that were derived on purely behavioral grounds: the theory of selection, optimization, and compensation (SOC; see Baltes, 1997) and socioemotional selectivity theory (SST; see Carstensen, Isaacowitz, & Charles, 1999). After discussing CRUNCH and its empirical foundations, we close with some speculations that it is hoped will point to future research that considers the dynamic reciprocity inherent in the co-constructive approach.

REALITY OF NEURAL AND COGNITIVE DECLINES

In various places throughout this chapter, we distinguish between the aging mind and the aging brain, recognizing the separable disciplines that have generated largely independent descriptions and accounts of the aging process. Neurobiological descriptions of the aging process emphasize structural changes, along with functional alterations, that are measured physiologically. This approach, largely devoid of reference to psychological function, is what we refer to as the aging brain. Conversely, the psychological accounts of the aging process emphasize functional changes in the performance of the “system.” Psychological theories explain performance changes by appealing to psychological constructs, mental operations, and the environmental/experiential dynamics that shape them, with minimal reference to neurobiological substance that embodies and implements these processes. This approach is captured by our phrase “the aging mind.”

In truth, as cognitive neuroscientists, we believe this to be a false dichotomy in that mental events have an underlying neurobiology that can influence other neurobiological processes, neurobiological processes give rise to mental events, and our methods enable us to investigate both levels of analysis in tandem. Nevertheless, the dichotomy recognizes the disciplinary boundaries that have largely characterized the study of aging, with emphasis on behavioral/performance measures and psychologically based theories on the one side, versus neural and biologically based explanations on the other.

Aging is accompanied by global declines in brain structure as well as specific and localized alterations (for a review, see Raz, 2000). On the macro level, brain weight and volume decline approximately 2% per decade in a relatively linear fashion. This decrease is related to the expansion of the cerebral ventricles and the enlargement of the cerebral sulci. On a micro level, these declines in brain weight and volume are manifest in

neuron shrinkage; debranching of the dendrites; declines in synaptogenesis; declines in dopamine receptors, transporters, and storage vesicles; and generalized white and gray matter loss.

It is also recognized that atrophy of the aging brain is not fully global and that some areas are more affected than others. In the neocortex, the prefrontal association cortex is especially vulnerable to age-related atrophy relative to more moderate declines in the temporal, parietal, and occipital cortices and minimal age-related decline in the anterior cingulate gyri. Moreover, lateral prefrontal areas may be more affected than orbital frontal cortex, an effect that has interesting implications given the divergent trajectories of cognitive decline and emotional preservation and improvement.

Differential age-related atrophy is also evident subcortically. Moderate shrinkage of the amygdala, hippocampus, mammillary bodies, caudate, putamen, and globus pallidus have all been documented, whereas the pons appears less sensitive to the effects of age, at least with respect to volume. The extent to which these patterns of spared versus moderate to extensive neural atrophy align with patterns of preservation versus decline in the aging mind is the subject of vigorous and ongoing research.

The characterization of the aging mind has been strongly influenced by the psychometric tradition of intelligence testing. Accordingly, developmental psychologists conceive of the mind as a multidimensional system that is comprised of different intellectual abilities that have different life course trajectories (Schaie, 2005). In particular, decades of research on cognitive aging have documented a steady decline over the lifespan on tests that are believed to measure fluid intelligence, such as reasoning, problem solving, and tests of associative and recollective memory. In contrast, measures of knowledge-rich, crystallized intelligence, such as tests of vocabulary, numerical abilities, and world knowledge are relatively well preserved in older adults (for reviews, see Craik & Salthouse, 2000).

Several theories have been proposed to account for the differential effects of aging on these two broad classes of mental abilities. One sort of model appeals to the underlying construct of cognitive resources, such as processing capacity (i.e., mental workspace) or processing speed. Tasks that tap fluid intelligence are posited to be more resource demanding and more dependent on mental effort than measures of crystallized intelligence (Hasher & Zacks, 1979; Salthouse, 1996). Consequently, performance changes due to aging will be more evident on tasks that are resource dependent. A different but related view is that, relative to knowledge-based intellectual abilities, fluid facets of intelligence, also referred to as cognitive mechanics, are more constrained by the integrity of biological mechanisms (Baltes, 1997). Knowledge-based abilities are more exogenously influenced, contextualized, and closely linked to the cultural and experiential history of an individual. The biological declines that accompany aging are therefore more evident in measures of fluid intelligence.

The information processing tradition of cognitive psychology has fostered a characterization of the aging mind in terms of constituent mental operations or processes. This tradition emphasizes the use of “model” experimental paradigms to analyze elementary perceptual and cognitive processes that are viewed as the building blocks or constituents of complex mental abilities. The goal here is to identify the basic operations that are most affected by the aging process. One of the most influential accounts of this type proposed by Hasher and Zacks (1988) posits that a fundamental source of age-related changes in cognition is a decline in inhibitory processes. According to this view, aging reduces the ability to filter out irrelevant information, to delete no longer relevant information, and to resolve conflict between competing inputs and competing response tendencies. By considering such elementary mental operations as cognitive mechanics, it becomes possible to integrate the information processing view of cognitive aging with accounts arising from the psychometric tradition (see Li et al., 2004). There is a need for future research in aging and lifespan development to achieve a more thorough integration of the intellectual abilities framework and the information processing approach, especially in an effort to understand the neuropsychological basis of aging.

Nevertheless, the information processing approach to cognitive aging has lent itself to a more brain-based, neuropsychological framework in which to understand the aging mind. Although the psychometric tradition clearly recognizes that age-related changes in intelligence must have biological correlates, a focus on basic cognitive operations permits a more direct mapping to neurological mechanisms. Thus, the information processing approach has enabled a fertile integration of biological and behavioral approaches. From this perspective, researchers have tried to understand age declines by identifying similarities between the cognitive and task performance profiles of older adults and those obtained from patient populations who have well-described, circumscribed neurological deficits. One merit of this approach is that it has generated hypotheses that link cognitive declines in aging to alterations in specific neural subsystems. For example, aging of the hippocampus is viewed as a critical source of age declines in associative and recollective memory. Neural declines in prefrontal cortex are the hypothesized cause of declines in reasoning, problem solving, and the class of processes referred to as executive functions.¹ At the same time, analogies with the effects of brain damage have tended to promote a pessimistic view of the aging process that emphasizes loss rather than reorganization and the possibility of continued modifiability.

¹ Although a consensual definition of executive functions is lacking, most taxonomies include such processes as inhibition, planning, goal shifting, and rule formation and implementation (see Smith & Jonides, 1999, for a review).

More generally, behavioral analyses are associated with the temptation to assume that preserved performance indicates that the mechanisms underlying task performance are also preserved. Although the use of compensatory strategies has figured prominently in some accounts of cognitive aging (Bäckman & Dixon, 1992; Baltes, 1997), the equation of spared and impaired performance with spared and impaired underlying processes, respectively, has been the predominant neuropsychological approach to aging until recently. The interpretation of spared performance is especially important to consider because it could signal preservation of underlying circuitry, compensatory processes, or some combination thereof. By using brain imaging technology to assess neural activity while older adults are engaged in different cognitive tasks, it has become possible to identify the substrates of spared versus impaired performance, and to characterize the corresponding utilization of neural resources. The additional leverage, thus provided, has proven essential in the view we develop here about the role of compensation and functional reorganization in the circuitry that supports cognitive performance in older age (see also, e.g., Park et al., 2001).

PLASTICITY IN AGING

Against a backdrop of neural and cognitive declines, resilience, plasticity, and the capacity for reorganization endure through the latter decades of life according to multiple sources of evidence. One of the most direct ways to identify an enduring capacity for plasticity is to examine the effects of training interventions on the performance of older adults. Indeed, the ability of older adults to benefit from training and to acquire new skills well into the ninth decade of life were extensively studied and well established nearly two decades ago (Baltes & Lindenberger, 1988). For example, the method of loci, widely used to improve long-term memory, involves associating new materials with a series of well-known landmarks. Like most abilities, the ability to acquire new skills and the benefits of training interventions, such as the method of loci, decrease with age. Consequently, in training studies, age differences are most pronounced when skills have been learned and acquired to asymptotic levels (i.e., the method of testing the limits; Kliegl, Smith, & Baltes, 1990). Nevertheless, the capacity for improvement remains across the lifespan, and one goal of aging successfully is to achieve a full realization of one's potential for plasticity.

Of course, the seeds for successful aging are sown throughout the life cycle by experiential contexts that shape neural and cognitive functioning. There is accumulating evidence to indicate that the quality of cognitive functioning in older age is influenced by work experience (see Chapter 14), socioeconomic status, ethnicity, race, and culture (see Stern & Carstensen, 2000, for a review). The "training" benefits accrued and the "healthfulness"

promoted by particular life experiences and cultural contexts have been proposed as causal mechanisms underlying these effects. Yet, we are only beginning to understand the principles by which life experiences and the inputs and feedback from the environment shape the brain's structure and function. Here, we summarize recent cognitive neuroscience evidence demonstrating that even in older age there is sufficient plasticity to permit beneficial effects of experiential and environmental interventions that can promote successful aging.

The evidence for positively transformative effects of diet and exercise in older age is particularly exciting. Aging decreases the ability to combat chemical imbalances, such as increases in free radicals that damage cellular structure and have been compellingly linked to the deleterious effects of aging on the brain (Finch & Cohen, 1997). Antioxidants can correct such imbalances by deactivating these free radicals, thus preventing and potentially reversing the detrimental effects of aging. Specifically, dietary consumption of foods high in antioxidants – such as blueberries, strawberries, and spinach – have been shown not only to prevent the onset of neural and cognitive degradation, but also to reverse these decrements once already in motion (Joseph et al., 1999).

Apart from the benefits of weight control and an improved sense of well-being, a decade of research has established that higher levels of physical fitness can maintain and even enhance aspects of cognitive functioning (Churchill et al., 2002). Compared with older people who are low in cardiovascular fitness, highly fit seniors not only perform better on cognitive measures of attention and conflict resolution, but they also demonstrate more efficient recruitment of the neural circuitry critical for implementing cognitive control (Colcombe et al., 2004). There is some evidence to indicate that even a short-term program of aerobic exercise can actually reverse the downward trajectory that characterizes measures of fluid intelligence and effortful processing tasks (Churchill et al., 2002). Animal models have demonstrated that brain function is a direct recipient of the benefits of aerobic training through increased neurogenesis, and other neurophysiological changes that foster neuronal survival and plasticity (van Praag, Christie, Sejnowski, & Gage, 1999). Moreover, increased vascularity in physically fit individuals could also improve neurophysiological function (Churchill et al., 2002). The benefits of diet and exercise could also operate indirectly; that is, fit bodies may function self-sufficiently in that they require less monitoring and fewer cognitive resources, thereby making a larger share of cognitive resource available for cognitive activity (see, e.g., Li, Lindenberger, Freund, & Baltes, 2001).

Animal models have clearly established the importance of enriched environments on neural and behavioral development. Not only is such exposure vital in the early stages of the life cycle, but also its influence can persist in later life as well. The exposure of old mice and rats to complex

environments, for instance, with more opportunities to explore novel situations, objects, and social interactions, improves performance on cognitive and behavioral tasks (Winocur, 1998). Such behavioral improvements occur when the animals are moved from impoverished to enriched environments. Moreover, when the animals are moved from enriched to impoverished environments, opposite results emerge as declines in performance (Winocur, 1998). Thus, behaviorally it appears that the effects of the environment on behavior and cognition are somewhat reversible and plastic even in older age. There has been considerable progress in identifying the neural correlates associated with environmental influences in the mature adult brain. Enriched environments have been associated with synaptogenesis, dendritic branching, neurogenesis, and plasticity of supportive elements such as glial cells (see Churchill et al., 2002; Chapter 4). Plasticity of this sort is likely to underlie the behavioral and cognitive improvements observed in enriched environments into older age.

The factor of social engagement, which can be viewed as the mutual and interactive influence of experiential and environmental factors, has also been shown to influence the aging process. For instance, high levels of social engagement, such as living with a spouse and/or having monthly contact with close family members or friends, improve performance on measures of cognitive ability (Arbuckle, Gold, & Andres, 1986). It may not be the actual social contact that prevents cognitive decline, but rather the social and emotional support received (Seeman, Lusignolo, Albert, & Berkman, 2001).

It is part of the co-constructivist argument that neural and cognitive aging are contingent on extant cultural conditions. Although the mechanisms have yet to be elucidated, neural aging must also reflect the cultural and technological context in which the biology of aging takes place. The fact that vitality and longevity have been extended and continue to be extended must entail fundamental changes in the characteristics of the aging brain. In turn, the presence of an older citizenry within a culture will shape the characteristics of that culture. Although an extensive review of cultural influences on aging is outside the scope of this chapter (see Chapter 2), it is helpful to consider how a “cultural neuroscience” approach to aging can test various hypotheses about the structure of aging cognition and the influence of environmental context. For example, the proposal that cognitive mechanics are more dependent on the integrity of biological mechanisms than knowledge-based intelligence (pragmatics) predicts marked age differences in the neural substrates of fluid intelligence measures along with relative cultural invariance. However, pragmatic aspects of intelligence should be associated with differences that are more pronounced between groups of older adults from different cultural backgrounds than between groups of younger adults (see Park & Gutchess, 2002; Park, Nisbett, & Hedden, 1999, for informative discussions of this research agenda).

In sum, the aging mind and brain exhibit persisting plasticity in response to experiential, environmental, and cultural factors. Although we are just beginning to understand the genetic characteristics that promote successful aging (see Chapter 11), a host of experiential and environmental factors have clear beneficial effects on neurocognitive functioning. However, such adaptive capacities must be understood against the backdrop of neural and cognitive aging processes that impose inevitable limitations on the changing organism. How do the realities of decline and plasticity interact to create a new stage of the life cycle that we identify as old age?

INTERACTIONIST AND CO-CONSTRUCTIVIST VIEWS OF SOC AND SST

The theory of lifespan development advanced by Paul Baltes and his collaborators (Baltes, 1997) incorporates several concepts that are echoed in the neural account of aging that we present in this section. These concepts are selection, optimization, and compensation. Within the Baltes framework, which is referred to as SOC, the impetus behind adaptive behavioral change is the changing dynamics in the biology–culture interactions mediated by brain and behavior development. One prominent driving force is the increase in “biological vulnerability” due to the aging process. Another is the impact of cultural learning. With the increase in biological vulnerability, regardless of whether wittingly, the individual responds with a strategy of becoming increasingly selective about the repertoire of behaviors and cognitive acts in which he or she will engage. By narrowing one’s options, and by allocating resources to the set of behaviors that reflect past developmental acquisitions (i.e., cultural learning) and are most adequate and suitable to one’s current life circumstances, one can optimize those behaviors – that is, they can be performed with the fullest force of effort, greatest allocation of resources, and highest quality possible. Overall, this strategy is a form of compensation in which one’s resources are not divided across multiple and less essential domains at their expense, but rather, in which the most essential acts are preserved through selective resource allocation. According to the SOC theory, in addition, selective optimization (e.g., practice) strengthens those means that are critical for achieving the selected actions.

One excellent example of SOC in action comes from a recent study by Li, Lindenberger, Freund, and Baltes (2001). This group investigated differences in the selective optimization of concurrent tasks in younger and older adults. Participants were asked to engage in simultaneous memorization and walking tasks, and were also trained in the usage of external aids. Overall, older adults prioritized the walking task over the memorization task. Furthermore, consistent with SOC, the researchers found that when difficulty was elevated for both tasks, only the younger adults successfully

implemented aids for the memorization task; conversely, only the older adults benefited from aids for the walking task. Thus, when the level of demand forces selectivity, older adults adopt a sensorimotor focus, thereby optimizing their performance on the task most vital to their safety.

The adaptive allocation of resources has also been demonstrated in the domains of emotional functioning and social interactions through the research program of Laura Carstensen and her colleagues (1999). Their group has shown that as people age, they place higher priority on goals related to emotional meaning, whereas younger adults emphasize intellectual, knowledge-related goals. For instance, with respect to social encounters, older adults prefer to interact with familiar social partners, as compared with unfamiliar ones, due to the emotional significance of closer relationships. According to Carstensen et al.'s (1999) socioemotional selectivity theory (SST), the shift from intellectual, knowledge-related goals to emotion-related goals results from a change in time perspective that comes with aging. Younger adults see time as expansive, whereas for older adults time is more limited, and their goals change accordingly. With an open-ended time perspective, such as that of younger adults, people seek new information and new social partners. In contrast, when time is perceived as limited, as is the case of older adults, goals related to emotional meaning are prioritized such that people seek regulated emotional states and emotionally meaningful social interactions. Because older adults perceive the end of life as much closer in time than do healthy younger adults, their limited time perspective fosters an increased focus on emotion-related goals.

Thus, a change in future time perspective is a causal factor according to SST. However, the increased focus on emotionally meaningful goals is associated with age-related alterations in basic information processing mechanisms (for a review, see Carstensen & Mikels, 2005). Older adults appear to direct their attention away from negatively valenced stimuli and toward positively valenced stimuli, a pattern not observed in younger adults. Furthermore, in both working (short-term) memory and long-term memory, older adults also show a bias for remembering positively valenced stimuli. Thus, social and emotional changes across the lifespan are postulated to be linked to basic changes in information processing. The causal links between emotional, motivational, and cognitive age-related changes remain unclear; however, the current body of empirical support for SST makes evident the reciprocal relationship between these factors.

SOC and SST share the central idea that the cognitive, emotional, and behavioral repertoire that distinguishes the older adult from the younger adult is not simply caused by an aging biological substrate. Instead the aging mind represents the outcome of co-construction by biological and cultural forces. In addition, the aging mind responds adaptively to the reality of its own aging; by so doing, it alters its own psychological architecture, and ultimately, the social and cultural milieu in which it thrives. Although

to date, neither of these theories has been explicitly examined from a brain science point of view, cognitive neuroscience research on aging cognition, from our lab and others, has discovered principles of adaptation, compensation, and compromise that we believe stem from the brain's response to its own aging process, rather than reflecting a passive consequence of biological aging. In this sense, our brain-based approach offers an additional perspective on the co-construction of the aging mind and brain. In our view, the results display consistency with some of the principles that have derived from research conducted within a more behavioral, cultural learning framework.

CRUNCH

Reuter-Lorenz, Stanczak, and Miller (1999) published a report, entitled "Neural recruitment and cognitive aging: Two hemispheres are better than one, especially as you age," which supports the basic idea that as we age, declining neural efficiency requires that more neural circuitry get recruited at lower levels of task demand compared with younger adults. This hypothesis, CRUNCH, has its roots in these earlier observations and proposes that older adults in general tend to recruit more neural resources for any given task than their younger counterparts. Therefore, older adults are more likely to reach their resource ceiling at lower levels of task demand than young adults.

This view is similar to arguments by behaviorally oriented, cognitive aging researchers discussed earlier in the chapter, who claim that diminishing resources increase the level of difficulty or effort required for older adults, relative to their younger counterparts. Now, through the combined use of cognitive tasks that are analytical with respect to the underlying processes and functional neuroimaging, we are in a position to delineate which neural processes decline and which processes compensate in older age, and to identify the costs of compensation. We believe this compensation can take at least two forms. We refer to one as compensation by recruiting "more of the same" neural process, whereby more time is devoted to a particular process, or whereby more neural nodes are used from a pool of nodes specialized for this process. The other form we refer to as compensation by "supplementary processes," whereby additional operations or strategies are recruited to compensate for deficiencies that render the usual circuitry insufficient to perform the task alone.

Indeed, there is evidence from neuroimaging studies of younger adults that principles like "more of the same" and "supplementary processes" seem to be implemented by the brain to meet increasing task demand. For example, when task difficulty is varied parametrically by increasing the number of items that have to be held in working memory (i.e., over a retention interval of 3–10 s), several studies have reported that activity in

task-relevant areas increases linearly as a function of set size (e.g., Jonides et al., 1998). This would be an example of recruiting “more of the same” neural circuits to meet increased task demand. Task difficulty can also be increased by requiring that the individual perform one or more additional operations at some stage during task processing. Explicit changes in task demands have been shown to recruit additional brain areas that map onto the kind of processing introduced into the task. For example, the introduction of response conflict can lead to activation of the anterior cingulate (Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003), whereas requiring subjects to reorder items in a list rather than recall them verbatim recruits lateral prefrontal regions (Postle, Berger, & D’Esposito, 1999).

In the older brain, where neural efficiency declines from the host of biological factors reviewed earlier in the chapter, it follows that optimal processing would require additional neural recruitment at lower levels of task demand compared with the younger brain. Thus, older brains should activate like younger brains performing a more demanding task. This age difference in activation is what we hypothesize to be the compensatory utilization of neural circuits. However, the net effect of this neural strategy in combination with age-related loss of neural resources is that fewer resources are available to meet the processing requirements of more complex tasks – this is the “crunch.” In general terms, the resource ceiling is reached to complete the cognitive operations required of more rudimentary tasks; as a result, performance on more complex tasks suffers from the lack of additional resources and from the more global adverse consequences of declining neural efficiency.

EMPIRICAL BASES OF CRUNCH

One of the most exciting discoveries that has emerged from the use of neuroimaging to study aging cognition is finding that neurologically intact, healthy older adults show signs of overactivation – greater levels of activity – compared with younger adults performing the same task. Overactivity was an unexpected outcome because, given the shrinkage of neural tissue and the lesion model framework of cognitive aging, it was assumed that older brains would be less able than younger brains to engage the relevant circuitry, leading to underactivation as the dominant age-specific pattern. Indeed, overactivation in some brain regions is sometimes found to be accompanied by underactivation in others. Of paramount importance is that in many studies these age-unique activity patterns are the neural correlates of preserved performance, and several studies have now linked overactivation to high-performing subgroups of older adults (see Reuter-Lorenz & Lustig, 2005, for a review).

Not surprisingly, the majority of neuroimaging studies on cognitive aging have focused on memory; therefore, this is the domain in which

age-related overactivation is most widely reported (see Cabeza, Nyberg, & Park, 2005, for reviews). Initial studies using positron emission tomography (PET; see, e.g., Chapter 11) reported overactivation in the left frontal regions of older adults during retrieval from long-term memory, which typically activates right frontal sites in younger adults. With PET, it is not possible to eliminate the activation associated with erroneous trials. Because older adults make more errors than younger adults, the contributions of age versus differing performance level can be confounded. One study on spatial working memory from our lab (Reuter-Lorenz et al., 2000) got around this problem by selecting older adults who performed as well as or better than younger adults. We found that older adults showed more left hemisphere activation on this spatial task, which activated primarily right hemisphere sites in younger adults. That is, older adults showed activity that was more bilateral than younger adults, and the sites of overactivation were localized to regions of prefrontal cortex – brain regions that are activated by younger adults in response to higher task demands.

To date, regions of overactivation have characterized the activity patterns of older relative to younger adults across a wide range of tasks, including perceptual and attentional tasks, tests of language processing, tests of motor control, verbal working memory, episodic memory encoding, and autobiographical memory (see Reuter-Lorenz & Lustig, 2005). The sites of additional activity in older adults are frequently found in approximately mirror symmetric regions in the hemisphere opposite to the most active sites in younger adults, which yields a pattern of reduced asymmetry in older adults (Fig. 12.1). However, bilaterality is not always the dominant pattern, and in many cases, older adults tend to overactivate regions of prefrontal cortex. Of course, the pressing question is “What functions are served by regions of overactivation?” We briefly consider several interpretations, including the one that we favor, which is the possibility that these regions function in a compensatory manner (see also Grady & Kapur, 1999).

One obvious possibility is that older adults are engaging different and possibly more numerous cognitive strategies than younger adults. In its simplest form, we find this explanation to be inadequate. In our neuroimaging studies of working memory, using both self-report and performance measures of strategy use, we found no differences between the two age groups. In some reports, the stimulus materials used are so basic (e.g., Gabor patches of selected spatial frequencies) that they do not readily lend themselves to multiple strategies (see Reuter-Lorenz, 2002, for a review). Moreover, at least one report examining episodic memory has shown underactivation in older adults relative to younger adults when no strategy was provided, as well as bilateral activation in older relative to younger adults when both groups were given a specific encoding strategy (Logan, Sanders, Snyder, Morris, & Buckner, 2002). Another possibility is that older adults are simply trying harder than younger adults,

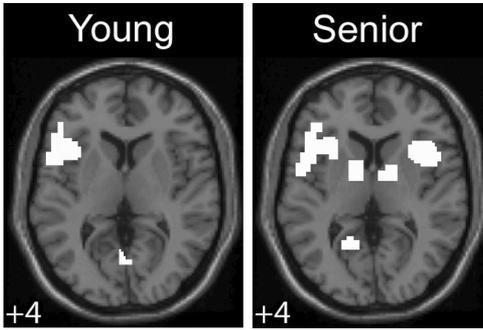


FIGURE 12.1. Horizontal sections showing BOLD activity obtained in younger (left-hand panel) and older (right-hand panel) adults. These images indicate the regions that are uniquely activated by a verb generation task condition that has high selection/interference resolution demands compared with a less demanding verb generation condition. In younger adults, activation is evident in the left inferior frontal gyrus. A pattern of age-specific overactivation is evident in the older adults who show bilateral activity in the left and right inferior frontal gyrus, and bilateral activation of the basal ganglia. Older adults are slower at verb generation overall compared with younger adults; however, the effect on performance of increasing the selection demand does not differ between the two age groups. We interpret the pattern of overactivation that occurs in the context of comparable performance effects to be consistent with compensatory processes in older adults. For more details, see Persson et al. (2004).

and this greater effort is manifest neurally as more active sites. One recent study addressed this possibility in the motor domain, using grip strength as the performance measure of interest. Both older and younger adults were asked to grip a dynamometer using their maximum grip strength, and then were scanned while gripping with different percentages of that maximum. The fact that the output was tailored to the ability level of each individual makes it difficult to account for the age-unique activation patterns by claiming that older adults expended more effort than younger adults (Ward, Brown, Thompson, & Frackowiak, 2003).

So, on what basis can we claim that these additional sites of overactivation in older adults are functioning in a compensatory manner? We offer four types of evidence that support this interpretation. First, there have been reports from studies of patients with focal lesions that indicate that certain language abilities lost after left hemisphere damage may be subsequently regained because the function has been taken over by the right hemisphere (see Reuter-Lorenz, 2002, for a review). Indeed, neuroimaging of patients with preserved language abilities after focal damage has revealed increased activity in right hemisphere regions homologous to the damaged sites but not typically associated with these abilities. Data such as these establish compensatory potential at the neurocognitive level.

A second piece of evidence comes from our own behavioral studies of older adults that used the divided visual field methodology to evaluate age-related changes in interhemispheric cooperation. Because of the way the left and right visual fields are mapped onto the retinas, it is possible to project initially to one side of the brain or the other. Consider a task in which a subject has to decide whether two items match, based on their physical appearance. Presenting the two items of such physical matches to the same visual field, thereby projecting to the same hemisphere, elicits better performance than when the items are presented to different visual fields. If the match is made more difficult by increasing the number of items or by requiring an abstract property such as the name of an item, it becomes advantageous for the items to appear in opposite visual fields, thereby engaging both hemispheres in the matching process. This is known as the bilateral field advantage. We have shown that, relative to younger adults, older adults show a stronger bilateral field advantage at lower levels of task demand (Reuter-Lorenz et al., 1999). We interpret this result to indicate that older adults benefit from engaging more neural circuitry and that this increased recruitment serves to compensate for declining neural efficiency.

The third piece of evidence supporting the compensation interpretation is the link between overactivation found in brain imaging studies of episodic and working memory and higher performance levels in senior subjects. In at least three studies of working memory, increased prefrontal activation has been correlated with higher levels of performance in older adults (see Reuter-Lorenz & Sylvester, 2005, for a review). Likewise, in studies of episodic memory that have examined high- and low-performing subgroups of seniors, the higher-performing subgroup has been the one showing greater overactivation (see Reuter-Lorenz & Lustig, 2005, for a review). Results such as these challenge the proposal that overactivation is a sign of neural dysfunction (due possibly to a breakdown in inhibition) and that it plays a causal role in impaired performance in older age (see Reuter-Lorenz, 2002; Reuter-Lorenz & Lustig, 2005). Finally, the neural correlates of cognitive processing can now be examined on a trial-by-trial analysis using event-related functional magnetic resonance imaging. Using this approach, researchers have been able to separately analyze the activation patterns associated with mnemonic encoding that ultimately lead to successful versus unsuccessful memory retrieval. To date, *successful* memory encoding has been associated with greater activation in prefrontal cortex in older adults than in younger adults. The activation is either bilaterally distributed or right localized, and it co-occurs with diminished activity in medial temporal lobe regions, suggesting that the prefrontal activity serves to compensate for age-related diminution of hippocampal efficiency (see Reuter-Lorenz & Lustig, 2005, for a review).

Ongoing research is now attempting to link sites of overactivation to specific neurocognitive processes to determine how compensation occurs, and whether a particular patterns falls into the “more of the same,” the “supplementary processes,” or some other category. In cases where there is additional activation in homologous regions of the cortex, as we have found in both dorsolateral and inferior frontal gyri, compensatory recruitment of the “more of the same” cognitive process is arguably the most plausible interpretation. However, in cases where frontal overactivation accompanies hippocampal underactivation, for example, the “additional process” interpretation would seem more compelling. Indeed, the fact that overactivation in seniors is frequently found in prefrontal sites has been taken as evidence that older adults rely on executive processes to a greater extent than do younger adults (see Reuter-Lorenz & Lustig, 2005). Likewise, on the basis of behavioral results, Baltes, Lindenberger, and their colleagues have proposed that pragmatic aspects of intelligence, including knowledge-based and strategic processes, are relied on extensively to compensate for declines in cognitive mechanics that are more vulnerable to age-related biological loss (e.g., Li et al., 2004). More work is needed to map the pragmatic/mechanic distinction onto such taxonomies as those applied to the central executive, where inhibition, selection, and goal shifting are defined as executive functions. In any case, a neuroimaging approach to cognitive aging should be able to evaluate this and other proposals in the future when a more thorough linkage of cognitive operations to specific activations patterns has been achieved.

So, what evidence exists to indicate that overactivation in older adults comes at an eventual cost? To date, there is little in the way of neuroimaging data to support this idea. According to CRUNCH, the lower the level of task demand for which additional recruitment must occur, the lower the level of task demand for which the resource ceiling will be reached. At higher levels of task demand, recruitment could reach asymptotic levels and, having reached this capacity limit, there is no further benefit to performance. There is at least one study of dual task performance that has related extensive recruitment in older adults on the single task conditions to underactivation and poorer performance in the dual task condition (DiGirolamo et al., 2001). More data along these lines are needed to test the resource limitation ideas of CRUNCH. In addition, neural efficiency is likely to depend on the effectiveness of connectivity or communication between task-relevant regions, as well as levels of regional activity. A full evaluation of CRUNCH will also require an extensive examination of the relationship between connectivity, activation levels, and performance.

IMPLICATIONS FOR ENVIRONMENTAL–CULTURAL CHANGE

The dramatic increase in human life expectancy since the early 1900s holds the promise of richer, fuller, and longer lives. What new insights have

emerged from studying the aging mind and its neural underpinnings that can improve the way we age? How can we reframe our understanding of the lifelong developmental process to foster more successful aging? We believe that appreciating the recursive nature of the aging process offers a pivotal insight: when we study the aging mind and brain, we are investigating a system that reflects in its outcome the result of past experiential and cultural learning and, in the context of the present, responds to its own aging. The measurements we take, whether they are behavioral or neural, are not mere indices of the consequences of biological aging in the narrow sense. They include the enduring plastic effects of the mind and brain as these systems adapt, reorganize, select, prioritize, and compensate in response to biological aging and environmental pressures. Behavioral measures constitute the end product of these dynamics and thus defy a one-to-one mapping with underlying mechanisms.

Consider a key lesson from neuroimaging: some tasks that are spared in subgroups of older adults, such as the short-term retention of spatial locations, are accomplished by a different neurocognitive route than when the task is performed by the younger brain. Spared performance does not imply that the underlying circuitry is unaltered due to aging. Rather, sparing of performance, the output of the system if you will, may well result from the brain's ability to allocate the necessary neural resources to the storage operations required by this task. Although the precise resources that are used are currently unknown, executive operations and increased cognitive control are likely candidates to be recruited to assist with and supplement rudimentary subtasks, such as storage, that in younger years did not require this additional support. This hypothesis implies that processes that are relatively resource free in the younger brain become more resource intensive in the older brain. Processes can appear spared in older adults because the compensatory contributions of executive functions, for example, maintain the behavioral performance of older adults. However, the increased reliance on executive processes that characterizes aging cognition makes executive functions themselves increasingly vulnerable to overload. The idea derived from behaviorally oriented research that in later life there is a compensatory shift away from some cognitive functions, with increasing reliance on others, is clearly echoed in the brain imaging results of older adults.

So, if this is the state of affairs in the aging mind and brain, then what can we do to promote successful aging? First, we recommend engaging in conditions that produce automaticity in younger years and the persistence of this training into older age. Skill development and knowledge acquisition occur in stages that initially require deliberative and declarative processing but ultimately can become proceduralized and automatic. The larger the repertoire of automatic behaviors one develops over one's life course, the longer such behaviors can operate free of executive control (see Rogers,

as in the development of expertise, are highly domain specific (Kramer & Willis, 2002). Thus, the acquisition of a large and diverse repertoire of automatic behaviors would be necessary. By the same token, it will be important to rethink intervention strategies and methods for improving quality of life for the older generation. According to our hypothesis, one source of the “crunch” in aging comes from the increased need to allocate executive resources for low-level tasks. Thus, if interventions are targeted at these tasks, it will relieve some of the burden on executive processes. This approach is similar to providing environmental support to older adults to overcome their failure to self-initiate strategy use. (See Chapter 16 for an extensive treatment of the importance of co-constructive considerations for the development of assistive technologies.)

Second, we recommend lifelong training in executive skills. To the extent that these processes become the backbone of cognition in later years, their optimization in early years can increase their endurance and youthfulness. Recent support for this speculation comes from a study of bilingualism and aging (Bialystok, Craik, Klein, & Viswanathan, 2004). Older adults who were bilingual showed better performance on measures of executive control than age-matched monolingual individuals. These performance differences emerged despite the fact that groups were otherwise indistinguishable on other critical measures, including education, vocabulary, intelligence, and basic measures of working memory. Bialystok and her colleagues argued that the increased cognitive demands presented by the requirement to adjudicate between two languages fosters the development of executive control processes, which in turn protect against some cognitive effects of aging. One potential future use of neuroimaging methods can be to identify the operations that function in a supplemental, compensatory fashion and to train or exercise these operations throughout life to ensure their viability in older age.

The multiple arguments in favor of lifelong physical fitness need not be reiterated here, except to say that the benefits of cardiovascular fitness and good diet on mental fitness in older age are striking. New evidence suggests that fit seniors are more apt to engage task-relevant brain regions, and thus may be less reliant on compensatory neural strategies than their less fit peers (Colcombe et al., 2004). Furthermore, given the evidence that physical challenge exacts a larger cognitive toll in older than younger adults (Li et al., 2001), the sense of physical well-being that comes with physical fitness means a greater availability of neurocognitive resources for cognitive rather than physical effort.

In summary, we argue for the optimization of biocultural and co-constructive processes across the lifespan so as to render brain status high. Plasticity of the brain and plasticity of the environment-driven input-output conditions create brain resources that endure across the lifespan. As we supplant the myths of aging with a deeper understanding of the

cognitive, affective, and neurobiological processes at work, we can develop educational goals that include a proactive approach to aging and the shaping of the brain. We can begin to shift the focus of our youth-oriented culture to one that is oriented toward the lifespan. Our understanding of living well can expand beyond eating well and exercising to include thinking well and establishing the cognitive foundations that optimize our mental machinery for the later years. Such cultural change can promote the benefits of mind–brain reciprocity so the brain’s response to its own aging and the demands posed by environmental conditions are influenced by the mind’s understanding of itself as a changing body in a changing environment.

ACKNOWLEDGMENTS

We thank Sam Maglio and Laura Zahodne for their valuable assistance with the preparation of this chapter and Jonas Persson for his comments on an earlier version of this manuscript. We acknowledge the support of the National Institute on Aging with research grant AG18286 to PARL and Ruth L. Kirschstein National Research Service Award AG022264 to JAM.

References

- Arbuckle, T. Y., Gold, D., & Andres, D. (1986). Cognitive functioning of older people in relation to social and personality variables. *Psychology and Aging, 1* (1), 55–62.
- Bäckman, L., & Dixon, R. A. (1992). Psychological compensation: A theoretical framework. *Psychological Bulletin, 112* (2), 259–283.
- Baltes, P. B. (1997). On the incomplete architecture of human ontogeny: Selection, optimization, and compensation as foundation of developmental theory. *American Psychologist, 52* (4), 366–380.
- Baltes, P. B., & Lindenberger, U. (1988). On the range of cognitive plasticity in old age as a function of experience: 15 years of intervention research. *Behavior Therapy, 19* (3), 283–300.
- Bialystok, E., Craik, F. I. M., Klein, R., & Viswanathan, M. (2004). Bilingualism, aging, and cognitive control: Evidence from the Simon task. *Psychology and Aging, 19* (2), 290–303.
- Cabeza, R., Nyberg, L., & Park, D. (Eds.). (2005). *Cognitive neuroscience of aging: Linking cognitive and cerebral aging*. London: Oxford University Press.
- Carstensen, L. L., Isaacowitz, D. M., & Charles, S. T. (1999). Taking time seriously: A theory of socioemotional selectivity. *American Psychologist, 54* (3), 165–181.
- Carstensen, L. L., & Mikels, J. A. (2005). At the intersection of emotion and cognition: Aging and the positivity effect. *Current Directions in Psychological Science, 14* (3), 117–121.
- Churchill, J. D., Galvez, R., Colcombe, S., Swain, R. A., Kramer, A. F., & Greenough, W. T. (2002). Exercise, experience and the aging brain. *Neurobiology of Aging, 23* (5), 941–955.

- Colcombe, S. J., Kramer, A. F., Erickson, K. I., Scalf, P., McAuley, E., Cohen, N. J., et al. (2004). Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National Academy of Sciences (USA)*, 101 (9), 3316–3321.
- Craik, F. I. M., & Salthouse, T. A. (Eds.). (2000). *The handbook of aging and cognition* (2nd ed.). Mahwah, NJ: Erlbaum.
- DiGirolamo, G. J., Kramer, A. F., Barad, V., Cepeda, N. J., Weissman, D. H., Milham, M. P., et al. (2001). General and task-specific frontal lobe recruitment in older adults during executive processes: A fMRI investigation of task-switching. *Neuroreport*, 12 (9), 2065–2071.
- Finch, C. E., & Cohen, D. M. (1997). Aging, metabolism, and Alzheimer's disease: Review and hypotheses. *Experimental Neurology*, 143, 82–102.
- Gehlen, A. (1988). *Man, his nature and place in the world*. New York: Columbia University Press.
- Grady, C. L., & Kapur, S. (1999). The use of neuroimaging in neurorehabilitative research. In D. T. Stuss, G. Winocur, & I. H. Robertson (Eds.), *Cognitive neurorehabilitation* (pp. 47–58). New York: Cambridge University Press.
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, 108 (3), 356–388.
- Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 22, pp. 193–225). San Diego: Academic Press.
- Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., et al. (1998). The role of parietal cortex in verbal working memory. *Journal of Neuroscience*, 18 (13), 5026–5034.
- Joseph, J. A., Shukitt-Hale, B., Denisova, N. A., Bielinski, D., Martin, A., McEwen, J. J., & Bickford, P. C. (1999). Reversals of age-related declines in neuronal signal transduction, cognitive, and motor behavioral deficits with blueberry, spinach, or strawberry dietary supplementation. *Journal of Neuroscience*, 19 (18), 8114–8121.
- Kliegl, R., Smith, J., & Baltes, P. B. (1990). On the locus and process of magnification of age differences during mnemonic training. *Developmental Psychology*, 26 (6), 894–904.
- Kramer, A. F., & Willis, S. L. (2002). Enhancing the cognitive vitality of older adults. *Current Directions in Psychological Science*, 11 (5), 173–177.
- Li, K. Z. H., Lindenberger, U., Freund, A. M., & Baltes, P. B. (2001). Walking while memorizing: Age-related differences in compensatory behavior. *Psychological Science*, 12 (3), 230–237.
- Li, S.-C., Lindenberger, U., Hommel, B., Aschersleben, G., Prinz, W., & Baltes, P. B. (2004). Transformations in the couplings among intellectual abilities and constituent cognitive processes across the life span. *Psychological Science*, 15 (3), 155–163.
- Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron*, 33 (5), 827–840.
- Nelson, J. K., Reuter-Lorenz, P. A., Sylvester, C. Y., Jonides, J., & Smith, E. E. (2003). Dissociable neural mechanisms underlying response-based and familiarity-based conflict in working memory. *Proceedings of the National Academy of Sciences (USA)*, 100 (19), 11171–11175.

- Park, D. C., & Gutchess, A. H. (2002). Aging, cognition, and culture: A neuroscientific perspective. *Neuroscience & Biobehavioral Reviews*, 26 (7), 859–867.
- Park, D. C., Nisbett, R., & Hedden, T. (1999). Aging, culture, and cognition. *Journals of Gerontology: Psychological Sciences & Social Sciences*, 54B (2), P75–P84.
- Park, D. C., Polk, T. A., Mikels, J. A., Taylor, S. F., & Marshuetz, C. (2001). Cerebral aging: Integration of brain and behavioral models of cognitive function. *Dialogues in Clinical Neuroscience*, 3 (3), 151–165.
- Persson, J., Sylvester, C. Y., Nelson, J. K., Welsh, K. M., Jonides, J., & Reuter-Lorenz, P. A. (2004). Selection requirements during verb generation: Differential recruitment in older and younger adults. *NeuroImage*, 23, 1382–1390.
- Postle, B. R., Berger, J. S., & D'Esposito, M. (1999). Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. *Proceedings of the National Academy (USA)*, 96 (22), 12959–12964.
- Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. I. M. Craik & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (2nd ed., pp. 1–90). Mahwah, NJ: Erlbaum.
- Reuter-Lorenz, P. A. (2002). New visions of the aging mind and brain. *Trends in Cognitive Sciences*, 6 (9), 394–400.
- Reuter-Lorenz, P. A., Jonides, J., Smith, E. E., Hartley, A., Miller, A., Marshuetz, C., & Koeppe, R. A. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience*, 12 (1), 174–187.
- Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: Reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, 15 (4), 245–251.
- Reuter-Lorenz, P. A., Stanczak, L., & Miller, A. C. (1999). Neural recruitment and cognitive aging: Two hemispheres are better than one, especially as you age. *Psychological Science*, 10 (6), 494–500.
- Reuter-Lorenz, P. A., & Sylvester, C.-Y. C. (2005). The cognitive neuroscience of working memory and aging. In R. Cabeza, L. Nyberg, & D. C. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 186–217). London: Oxford University Press.
- Rogers, W. A. (2000). Attention and aging. In D. C. Park & N. Schwarz (Eds.), *Cognitive aging: A primer* (pp. 57–73). Philadelphia: Psychology Press.
- Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, 103 (3), 403–428.
- Schaie, K. W. (2005). *Developmental influences on adult intelligence: The Seattle Longitudinal Study*. London: Oxford University Press.
- Seeman, T. E., Lusignolo, T. M., Albert, M., & Berkman, L. (2001). Social relationships, social support, and patterns of cognitive aging in healthy, high-functioning older adults: MacArthur Studies of Successful Aging. *Health Psychology*, 20 (4), 243–255.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, 283 (5408), 1657–1661.
- Stern, P., & Carstensen, L. L. (Eds.). (2000). *The aging mind: Opportunities in cognitive aging*. Washington, DC: The National Academies Press.

- van Praag, H., Christie, B. R., Sejnowski, T. J., & Gage, F. H. (1999). Running enhances neurogenesis, learning, and long-term potentiation in mice. *Proceedings of the National Academy of Sciences (USA)*, 96 (23), 13427–13431.
- Ward, N. S., Brown, M. M., Thompson, A. J., & Frackowiak, R. S. J. (2003). Neural correlates of motor recovery after stroke: A longitudinal fMRI study. *Brain*, 126 (11), 2476–2496.
- Willis, S. L., & Nesselroade, C. S. (1990). Long-term effects of fluid ability training in old-old age. *Developmental Psychology*, 26 (6), 905–910.
- Winocur, G. (1998). Environmental influences on cognitive decline in aged rats. *Neurobiology of Aging*, 19 (6), 589–597.