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Executive Functions and Neurocognitive Aging

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O U T L I N E

OVERVIEW

Executive functions (EFs) play a fundamental, yet poorly understood, role in neurocognitive aging. The overarching goal of this chapter is to consider both sides of that statement. That is, we will review behavioral and neuroimaging evidence indicating the centrality of executive functioning to cognitive aging, and we will also delineate some of the major barriers or puzzles that challenge a coherent and thorough account of the role of EF in aging. Finally, we will

consider how and to what extent declines in EFs affect typical day-to-day activities of older adults.

EFs are multifaceted control processes that regulate thought and behavior. While different taxonomies have been proposed to account for the range of processes that are "executive" in nature, EFs typically refer to a family of general-purpose mechanisms (i.e., updating, inhibiting, switching, working memory, prioritizing, sequencing), largely mediated by the prefrontal cortex (PFC), that are critical to other higher cognitive abilities including planning, reasoning, long-term memory, decision making, and problem solving. The implementation of EFs entails dynamic interactions among neural populations within and between the left and right frontal lobes themselves, along with circuits in other cortical areas, especially the parietal lobes, and subcortical regions, including the thalamus, basal ganglia, limbic system, midbrain, and the cerebellum. Thus, neuroanatomical considerations of EFs concentrate largely on the structure and function of the frontal lobes, however, frontal areas are critical nodes in a more complex network of cortical and subcortical regions that implement executive control (Fuster, 2013).

MEASURING EFs

Numerous tasks can be used to measure EFs and these can be divided into two general classes. One class includes *standardized neuropsychological instruments* that are often part of a larger test battery used to characterize the cognitive status of a given research population. Such EF measures include Trail Making (especially Trails B; see, e.g. Lezak, 2004), Wisconsin Card Sorting, Stroop (Stroop, 1935), measures of verbal fluency (e.g., COWT; Ivnik, Malec, Smith, Tangalos, & Petersen, 1996), Wechsler Digit Span, and Letter-Number Sequencing (Wechsler, 1997). Neuropsychological measures

of this type have been used in a popular battery developed by Elizabeth Glisky and her colleagues to characterize healthy older adults in terms of the extent to which they display "frontal-executive" deficits, versus "medial-temporal-memory" deficits (Davidson & Glisky, 2002; Glisky & Kong, 2008; Glisky, Polster, & Routhieaux, 1995). The other class of measures includes *experimental tasks*, which are typically non-standardized, computerized tasks that analyze behavioral responses to specific stimulus manipulations. There are too many tasks of this type to list here, but common examples include the n-back (Kirchner, 1958), stop signal (Logan, 1994), anti-saccade (Hallet, 1978), AX-CPT (Braver et al., 2001), task switching (Rubinstein, Meyer, & Evans, 2001), and recent probes tasks (Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998).

While cognitive tasks are rarely "process pure," the impurity problem is especially relevant for measures of EF. As Miyake and Friedman (2012) point out, the target EF being measured by a task needs something to operate on—EFs are deployed in a cognitive context. To address this issue, one approach that both standardized and experimental measures of EF commonly employ is to compare a condition presumed to entail a specific executive demand to one that is otherwise identical but lacks the executive demand. For example, the Stroop task will include a baseline color naming condition without interference from color words, and the response time difference between baseline and color-word reading provides an index of susceptibility to interference. Similarly, in the n-back task, performance can be compared when participants have to hold and update information within working memory (i.e., during a 2-back task) to a condition in which they simply have to indicate if the stimulus is the same or different from a constant target stimulus (i.e., during a 0-back task). Further, a latent variable approach can be used to address the impurity problem with statistical methods that

extract common variance across multiple tasks targeting the same putative EF (Hull, Martin, Beier, Lane, & Hamilton, 2008). For instance, McCabe, Roediger, McDaniel, Balota, and Hambrick (2010) explored the commonalities between performance on measures of mental control, mental arithmetic, verbal fluency, and the Wisconsin Card Sorting Test (WCST) by performing a confirmatory factor analysis to determine if and how well each task contributed to an underlying latent component denoting EF.

A number of different taxonomies or subtypes of EFs have been identified using these and other methods including dissociation procedures testing patients with localized brain damage, functional neuroimaging, and experimental task analyses. Although there is no consensus about which particular processes qualify as "definitive" EFs, there are several that emerge repeatedly in one form or another, especially in relation to cognitive aging. These are: interference control (inhibition), cognitive flexibility (task switching), and updating (Friedman & Miyake, 2004; Hull et al., 2008; Verhaeghen & Cerella, 2002). Working memory is often incorporated into notions of executive functioning although it is generally viewed as a system consisting of active storage or maintenance processes, that are closely aligned with executive control functions (such as updating, inhibiting, refreshing). Working memory is essential for goal maintenance, whereby actively held representations guide on-going and forthcoming behaviors in accordance with plans, context, and task relevance. Additional executive control concepts that have been especially important to cognitive aging include the distinction between proactive and reactive control (Braver, Paxton, Locke, & Barch, 2009), self-initiated processing (Craik, 1994), and monitoring operations (Ridderinkhof, Span, & Van Der Molen, 2002), all of which share the properties of being potentially domain general, higher-order processes that regulate and guide cognition.

EXECUTIVE DEFICIT THEORIES OF COGNITIVE AGING

One indication that EFs play a major role in understanding cognitive aging is the fact that at least four major theories place executive functioning front and center! Because these theories have been around for about 10 years or more in various renditions, they have been discussed extensively in other venues (Craik & Salthouse, 2011; Hofer & Alwin, 2008; Jurado & Rosselli, 2007). Nonetheless, they all continue to be tenable hypotheses that garner various forms of new support. Therefore, the next section briefly reviews the core ideas from each theory to provide a framework for interpreting more recent evidence about the behavioral and neural indices of EF discussed later in this chapter.

Inhibitory Deficit Theory (Hasher & Zacks)

Hasher, Zacks, and Bower (1988) and Hasher, Stolzfus, Zacks, and Rypma (1991) proposed that a core deficit in aging pertains to the ability to inhibit or suppress irrelevant or no-longer-relevant information. The theory was originally cast in relation to working memory and the considerable evidence that working memory capacity is reduced in older adults. Their view focused on the contents of working memory, emphasizing that inhibitory dysfunction left older adults with deficits in (i) preventing irrelevant information from entering working memory; (ii) deleting no longer relevant information from working memory; and (iii) restraining prepotent information from dominating in working memory. Inhibition is invoked to explain many aspects of perceptual and attentional selection, and efforts to identify a unitary or core inhibitory deficit in older adults that spans perceptual, memorial, and response domains have met with mixed success (Aslan, Bäuml, & Pastötter, 2007; Butler & Zacks, 2006; Camp, Pecher, & Schmidt, 2007; Kramer, Humphrey,

Larish, & Logan, 1994; see for review Lustig, Hasher, & Zacks, 2007 or Lustig & Jantz, 2014). However, the idea that deficits in the ability to control interference, especially in relation to the contents of working memory continues to receive considerable behavioral and brain-based support (Aguirre, Gómez-Ariza, Bajo, Andrés, & Mazzoni, 2014; Gazzaley, 2011; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Machado, Devine, & Wyatt, 2009; Scullin, Bugg, McDaniel, & Einstein, 2011; Zanto, Hennigan, Östberg, Clapp, & Gazzaley, 2010).

Goal Maintenance Deficit (Braver & West)

Based on her pioneering research with single-unit recordings in awake monkeys, Goldman-Rakic (1995) proposed that the primary and overarching function of the PFC is the representation of task-relevant goals in the absence of support from external stimuli—in other words, working memory representations. Variants of this view have been advanced by Miller and Cohen (2001) and by Braver and West (2008), who specifically propose that aging is associated with the declining ability to actively maintain goal representations in working memory, due to neurophysiological alterations in the lateral PFC. Consequently, older adults are not able to adequately control top-down strategic processing, processing that is especially needed for tasks that involve conflicting perceptual or response demands. Braver and West also argue that a goal maintenance deficit can explain, or is at least compatible with, some aspects of memory decline evident in older adults, including deficits in associative binding (Naveh-Benjamin, 2000) and prospective memory (Henry, MacLeod, Phillips, & Crawford, 2004). Finally, Braver and West propose that effective goal maintenance is necessary for preparatory and flexible biasing of attention and action systems in dynamic environments—a process referred to as "proactive control," and contrasted with

"reactive control," where an effort is made to respond correctively, after the fact, rather than in an anticipatory fashion. A variety of evidence from continuous performance tasks, as well as some memory tasks, suggests that proactive control is especially difficult for older adults (Czernochowski, Nessler, & Friedman, 2010; Dew, Buchler, Dobbins, & Cabeza, 2012; Paxton, Barch, Racine, & Braver, 2008).

Production Deficit Hypothesis

The production deficit hypothesis is fundamentally related to the proposal made by Craik and Byrd (1982) that older adults are impaired at self-initiated, effortful processing—deficits thought to be linked to reduced cognitive and neural resources that in turn affect the learning and memory abilities of older adults (see also Kausler, Wiley, & Lieberwitz, 1992). Although this hypothesis does not map well onto the specific taxonomies of EFs (e.g., inhibition, updating, switching, etc.), it corresponds with the broader view that the frontal lobes are critical for strategic processing and the corollary that strategic deficiencies may contribute to age-related memory decline (Kirchhoff, Gordon, & Head, 2014; Naveh-Benjamin, Brav, & Levy, 2007). More importantly, perhaps, the enhanced ability to identify the neurocognitive processes that underlie memory encoding and retrieval, made possible by brain imaging methodologies, has established the fundamental importance of engaging prefrontal circuitry for successful memory (Fletcher & Henson, 2001; Moscovitch & Winocur, 1992; Paller, McCarthy, & Wood, 1988) and the prevalence of age-related differences in prefrontal recruitment during mnemonic tasks (Craik & Rose, 2012; Maillet & Rajah, 2014).

Frontal Lobe Hypothesis of Cognitive Aging

In 1996, West published a highly influential paper that reviewed extensive behavioral

and neuroscientific evidence supporting the hypothesis that declines in frontal lobe functions can explain a wide range of age differences in cognition. This hypothesis was grounded in earlier neuropsychological work based primarily on lesion studies that broadly compared the performance profiles of older adults to the types of deficits associated with damage to different brain regions (Albert & Kaplan, 1980; Dempster, 1992). As West pointed out, prior to his paper the major emphasis had been on inhibitory deficits, whereas his contribution broadened the explanatory scope of the frontal hypothesis of aging to acknowledge the heterogeneity of prefrontal subregions and the role of their representational abilities in controlling interference in attention and memory. One key tenet of this model is that deficits in frontally— mediated cognitive processes (i.e., EFs) should be the first and the earliest signs of cognitive aging to emerge across the lifespan— a prediction that is longitudinal in nature. A corollary of this prediction is that there will be time points, especially earlier in the course of aging, during which EFs are disproportionately affected.

A Current Perspective on Executive Deficit Theories of Cognitive Aging

The theories outlined above vary in the range of age differences they endeavor to explain, with the frontal lobe hypothesis of cognitive aging having the broadest reach. Overall these theories are not mutually exclusive and each is likely to have some piece of the truth about the nature of the cognitive deficits that can characterize older adults as a population. One crucial unknown, however, is whether there is one core executive deficit, such as impaired inhibition or working memory, that gives rise to other various manifestations of EF decline in cognitive aging. Some recent evidence pertaining to diminished resolution or clarity of working memory

suggests this possibility (Basak & Verhaeghen, 2011; Peich, Husain, & Bays, 2013; Verhaeghen & Zhang, 2012), and is consistent with prior structural equation modeling indicating the centrality of working memory function to cognitive aging (Charlton et al., 2008; Hull et al., 2008). Nevertheless, it remains doubtful that a single core executive deficit could account for the wide range of neuroanatomical and neurofunctional data that has emerged over the past decade or the vast individual differences in trajectories of cognitive decline (Carlson et al., 2008; Mungas et al., 2005; Park & Reuter-Lorenz, 2009; Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010; Wilson et al., 2002). Furthermore, it is increasingly evident that EFs are fundamental to maintaining high cognitive function in older age, and that compensatory cognitive and neural processes may ameliorate other deleterious biological and functional effects of aging (Reuter-Lorenz & Park, 2014). In the following sections we will consider the lifespan trajectories of EFs, as well as the compensatory support that may be conferred by utilizing preserved executive abilities in older age.

DO EFs SHOW THE EARLIEST AND DISPROPORTIONATE DECLINE?

One of the core assumptions in EF theories of cognitive aging is that EFs will be the first cognitive abilities to decline as people age, and that EF dysfunction will be disproportionally greater than other aspects of cognitive impairment. The first assumption requires longitudinal evidence to assess the trajectories of cognitive change within individuals, however the latter assumption could potentially be addressed with cross-sectional work assessing whether age-related differences in EFs are greater than those in other cognitive domains. We consider the cross-sectional evidence first.

Cross-Sectional Evidence for Disproportionate EF Decline?

Verhaeghen (2011) specifically examined whether age-related EF deficits were larger than age-related declines observed in non-executive comparison conditions. Using a series of meta-analyses based on the Brinley plot approach to assess differential age effects, Verhaegen reached two important conclusions regarding measures of resistance to interference, task coordination, and task shifting. First, with respect to absolute age differences, the effects of age were reliable and universally larger on executive versions of the tasks, compared to their respective non-executive conditions. Second, overall these deficits were not disproportional to the age effects measured on the comparison tasks. In other words, for most tasks analyzed, a single linear model fit the data for both versions of the task, which argues against a specific EF deficit per se, above and beyond that observed in the non-executive tasks. This was true for commonly used measures of EF, like Stroop and Trail Making. Several tasks did show specific EF deficits, namely reading with distraction, dual-tasking, and global task switching (see also Verhaeghen & Cerella, 2002; Note that global switching costs are generally thought to reflect the additional load entailed in actively maintaining two sets of task goals at the same time). However, one concern is that these effects were relatively modest, and another is that these tasks are not among the neuropsychological measures of EF typically used in large-scale studies of aging.

In a further set of analyses based on correlations among aggregated data from 119 published studies, Verhaeghen (2011) sought to determine whether declines in EF could account for age-related variance in other aspects of complex cognition as reflected in measures of episodic memory, reasoning and spatial ability, and how the variance accounted for compared to that explained by processing speed and working memory. Consistent with prior research (Park et al., 2002; Salthouse, 1991, 2005), speed and working memory accounted for a larger portion of the variance than EF (resistance to interference and task switching), and accounted for no variance independently of speed and working memory. Taken together, these analyses based on hundreds of cross-sectional studies suggest that key EFs, resistance to interference and task shifting, while clearly impaired in older adults, are neither disproportionately impaired compared with other cognitive functions, nor do they account for age-related variation in performance on other measures of complex cognition.

Nonetheless, working memory continues to emerge as an aspect of EF that, while strongly affected by age declines in processing speed, may play a fundamental role in other aspects of cognitive decline. Furthermore, given the relative paucity of studies on other putative EFs such as updating (Fisk & Sharp, 2004; Pelegrina, Borella, Carretti, & Lechuga, 2012; Schmitt, Ferdinand, & Kray, 2014) and other forms of interference control in memory that are clearly affected by age (i.e., semantic interference, proactive interference, directed forgetting; Hedden, 2001; Hogge, Adam, & Collette, 2008; Titz & Verhaeghen, 2010), the possibility that aspects of EF decline contribute prominently, and disproportionately to cognitive aging remains viable.

Longitudinal Evidence for Earlier EF Decline?

Increasing sets of longitudinal data are emerging relevant to the question of whether EFs show an earlier onset of decline compared to other domains of cognition and whether there are specific executive declines or solely global changes. Longitudinal studies have revealed that both domain-general and domain-specific changes exist (Tucker-Drob, 2011).

Although some variance in task performance can be captured by a general cognitive variable, performance on specific tasks, including tasks that require executive abilities, can account for remaining variance. Goh, An, and Resnick (2012) examined longitudinal cognitive trajectories in the Baltimore Longitudinal Study of Aging and observed varying patterns of cognitive change. Longitudinal declines were observed in many executive tasks, including verbal fluency, digit span, alpha span, and Trails B. These tasks require executive skills such as inhibition, mental manipulation of information in working memory, semantic retrieval, and switching between rule sets. This study also documented longitudinal declines in long-term memory. However, other measures of short-term memory, chunking, and discrimination assessed by the California Verbal Learning Test, as well as conceptual abstraction and working memory capacity, did not exhibit declines. This discrepancy may be due to differences in the difficulty of each task, differences in the types of processing required by each task, differences in vulnerability to test–retest practice effects, as well as due to individual differences in the experience of cognitive changes over time. Moreover, this variability in the longitudinal data reflects that declines in EF are not always observed, and, accordingly, that disproportionate declines in EF are also not ubiquitous.

Indeed, inter-individual variability in longitudinal trajectories has been documented in multiple studies (de Frias, Dixon, & Strauss, 2009; Goh et al., 2012; Wilson et al., 2002). Pertaining specifically to EF, de Frias et al. (2009) found individual differences in 3-year longitudinal changes in inhibition, shifting, and updating. Certain individuals had greater stability in EF, and these individuals had better EF abilities overall. Thus, important insights into the aging process may ultimately depend on understanding why individuals differ so widely in their trajectories of change.

DO BRAIN REGIONS LINKED TO EF SHOW THE EARLIEST AND DISPROPORTIONATE DECLINE?

If EFs are most vulnerable to age-related decline, then we might expect that the neural substrates of EF would show the earliest and most robust indications of the adverse effects of aging. In this section we consider evidence that bears on this claim. First, however, we review evidence linking age effects on EF to specific neuroanatomical substrates. As noted in the overview to this chapter, regions of PFC are known to play critical roles in EFs, and the body of research establishing these links includes studies of brain–behavior relations in patients with focal brain damage (Baldo, Delis, Wilkins, & Shimamura, 2004; Davidson, Gao, Mason, Winocur, & Anderson, 2008; Yochim, Baldo, Kane, & Delis, 2009) as well as functional imaging studies of regional brain activity during the performance of cognitive tasks (Collette et al., 2005; Funahashi, 2001; Koechlin & Summerfield, 2007). However, it is also clear that regions of PFC interact extensively with other cortical and subcortical areas (Fuster, 1997), making the integrity of white matter pathways that mediate these interactions a critical player in the effectiveness of prefrontal control. Research on the effects of aging highlights the critical role of these pathways.

Aging and the Neural Substrates of EF

Relationships between EFs and prefrontal structure, including measures of cortical thickness and volume of frontal subregions, and white matter pathology, have been documented in normal middle-aged and older adult populations. White matter hyperintensities (WMH) appear as bright spots on MRI images of the brain, and older adults frequently exhibit more WMH than younger adults (DeCarli et al., 1995). WMH have been associated with various

structural and functional brain changes, as well as increased clinical risk for stroke, dementia, and death (Debette & Markus, 2010). With regard to frontal lobe function, DeCarli et al. (1995) assessed WMH in adults free from other cerebrovascular risk factors and found evidence that greater levels of WMH were associated with reduced frontal lobe metabolism and worse performance on Trail Making Tests A and B (see also Tullberg et al., 2004). An early meta-analysis similarly related WMH and poor executive performance (Gunning-Dixon & Raz, 2000).

More recently, white matter integrity assessed using diffusion tensor imaging (DTI), has consistently revealed age-related declines in fractional anisotropy (FA) in the frontal lobes and links to EF decline (Grieve, Williams, Paul, Clark, & Gordon, 2007; Head et al., 2004; Kennedy et al., 2009; Salat et al., 2005). Low levels of FA reflect more disperse diffusion of water, which is indicative of decreased white matter integrity. For instance, Grieve et al. (2007) found evidence for a correlation between FA and EFs, such that lower FA values were associated with poor performance on the Trail Making task and a maze task (see also Brickman et al., 2006; Kennedy & Raz, 2009).

Critically, age-related cortical atrophy of PFC has also been linked to age-related EF impairment, sometimes in conjunction with white matter measures. In one early, widely-cited study Gunning-Dixon and Raz (2003) demonstrated that, in adults ranging in age from 50–86, both the volume of PFC and the integrity of underlying white matter (as indicated by quantification of WMH) predicted perseverative responses on the WCST (see also Kramer et al., 2007; Mungas, et al., 2005; Zimmerman et al., 2006). Consistent with this observation, Head et al. (2009) found smaller PFC cortical volumes to be associated with an increase in perseveration errors on the WCST. Measurements of other cortical regions did not share this predictive power.

A recent meta-analysis (Yuan & Raz, 2014) that includes 31 samples of participants with volumetric measures and 11 samples with measures of cortical thickness (total $N = 3272$ ranging in age from 18 to 85) confirms and extends this basic relationship, by showing that larger PFC measurements are associated with better EF performance. Although the effect sizes (as indicated by Cohen's d) were generally modest, the effects for WCST, interference, working memory, and digit span backward were all highly significant. Furthermore, measures of lateral PFC had the strongest relationship with performance. It is also noteworthy that bilateral PFC volumes have also been shown to predict the magnitude of EF decline over the course of 1 year in a non-demented older adult sample (ages 50–92; average age 73; Cardenas et al., 2011). A composite that included verbal fluency, Trail Making, and Stroop was used to measure EF, and decline was attributed largely to deterioration of white matter (Cardenas et al., 2011).

Taken together there is substantial evidence linking PFC volumes and measures of white matter degradation to levels of EF functioning in older adults. But are these indices of decline among the first to emerge over the course of late adulthood? We consider data relevant to that question in the next section.

Relative Degree and Onset of PFC Decline

Recent estimates of cortical volume reductions suggest a loss of approximately 0.02–0.03% per year, from about age 50 onward (Fjell et al., 2013). Of the age-related changes in brain structure that are commonly observed, structural changes in the frontal lobes have been thought to be the most dramatic (Brickman et al., 2006; Fjell et al., 2009; Grieve et al., 2007; Madden, Bennett, & Song, 2009; Raz et al., 1997; Salat et al., 2005), although there has also been considerable variability among studies due to a

variety of methodological and sampling issues (Raz & Rodrigue, 2006). Moreover, the majority of studies to date are cross-sectional, and, thus, they can only document differences related to chronological age. To reveal differences due to aging itself, longitudinal studies are required to assess within-individual changes in brain structure.

With respect to white matter, Head et al. (2004) provide evidence for an anterior–posterior gradient, such that frontal regions exhibit lower levels of white matter integrity and more posterior regions exhibit greater white matter integrity. An anterior–posterior gradient is consistent with the frontal lobe hypothesis, and has been found more generally in a meta-analysis by Madden et al. (2009) (see also Brickman et al., 2006).

Similar effects have been observed in the patterns of gray matter loss with age. Jernigan et al. (2001) report that the frontal lobes had a disproportionate reduction in cortical gray matter compared to the rest of the brain. A longitudinal study by Resnick, Pham, Kraut, Zonderman, and Davatzikos (2003) similarly reported a reduction in cortical gray matter over time. The largest gray matter losses were observed in the orbital frontal gyrus, inferior frontal gyrus, cingulate gyrus, insula, and inferior parietal gyrus. Further, though gray matter changes were observed in several regions across the course of 6 years, atrophy of frontal regions was associated with significant functional decline (Nyberg et al., 2010).

However, as Fjell et al. (2009) point out, given the wide variation in structural results, it is difficult to draw firm conclusions about whether prefrontal regions are more adversely affected by healthy aging than temporal cortex and medial temporal lobe regions, for example, which are also vulnerable to degenerative processes, especially associated with Alzheimer's disease (Clerx et al., 2013; Heckemann et al., 2011; Jack et al., 1997). To address this problem, the Fjell team (2009) culled data from 883 participants drawn from six different samples ranging in age from 18 to 93 years, and analyzed structural images using identical preprocessing and thresholding procedures. While age-related thinning of cortical tissue was evident throughout the cortex, age effects across samples were strongest and most consistent in prefrontal regions, especially superior, lateral and medial prefrontal regions, which are typically associated with EFs. These results are clearly consistent with the frontal lobe hypothesis of cognitive aging. The authors point out however, that the anterior cingulate, a medial structure considered to be part of the frontal lobes, was relatively preserved. This region is thought to contribute to error monitoring, and aspects of executive control associated with response inhibition and performance on the Stroop task (Botvinick, Cohen, & Carter, 2004; Pardo, Pardo, Janer, & Raichle, 1990).

Further, in one of the most extensive longitudinal studies of brain structures to date, Pfefferbaum et al. (2013) examined trajectories of change over a period of up to 8 years across multiple cortical and subcortical regions in over 100 cognitively normal individuals ranging in age from 20 to 85 at the time of their first scan. While decline was widely evident and tended to accelerate in older age, volume reductions in lateral and medial prefrontal regions were greater than in other cortical areas, including lateral and medial temporal regions, which also showed prominent age-related declines.

Based on the anatomical evidence it would seem that the frontal lobes are especially vulnerable to volume loss and white matter insults with age, a core assumption of the frontal lobe hypothesis of cognitive aging. The anatomical evidence as a whole may be more consistent and compelling than the cognitive-behavioral results, at least with respect to the question of earlier and disproportionate decline. This difference in sensitivity should not be surprising, perhaps, given the challenges the field has faced with identifying core EFs, along with

the great variation in tasks used to measure them. It also appears more generally that brain changes are likely to be measureable before cognitive changes in many domains (e.g., Mueller et al., 2005 regarding Alzheimer's disease; Raz et al., 2010; Raz & Lindenberger, 2011), suggesting that brain measures are more sensitive indicators of age-related decline than behavior. How then to reconcile the evidence for structural decline with what seems to be the many PFC-mediated strategic and compensatory processes engaged by older adults as revealed through functional brain imaging? We turn to that question next.

EFs AND PFC PROCESSES AS COMPENSATORY AND PROTECTIVE

Despite the structural indications that the frontal lobes are especially vulnerable to the adverse effects of aging, functional neuroimaging studies frequently reveal over-recruitment of the prefrontal regions in older adults, and some results have linked these effects to compensation and better performance in older adults (Cabeza & Dennis, 2012; Reuter-Lorenz & Cappell, 2008). That is, across a broad range of experiments measuring task-related activation with functional neuroimaging, older adults have been shown to activate frontal regions that are not active in younger adults performing the same tasks (Cabeza, 2002; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Gutchess et al., 2005; Reuter-Lorenz, 2002). Recently, Turner and Spreng (2012) used a meta-analytic activation likelihood technique to examine such age differences during executive tasks from 27 studies, resulting in a sample of 350 younger and older adults. They documented that activation was reliably greater in older adults in bilateral dorsolateral prefrontal cortex (DLPFC), supplementary motor cortex, and left inferior parietal lobule during working memory tasks. For

tasks that required inhibitory control, older adults tended to showed greater recruitment of the right inferior frontal gyrus and the presupplementary motor area. Similarly, a recent meta-analysis by Maillet and Rajah (2014) comparing age-related activation during *successful* memory encoding showed greater activation for older adults in bilateral middle frontal gyri, bilateral superior frontal gyri, anterior medial frontal gyri, precuneus, and the left inferior parietal lobe, when encoding new episodic memories that they could subsequently remember. These converging data from multiple studies demonstrate that older adults appear to increasingly depend on PFC, and that different specialized frontal networks are recruited depending on the type of executive demands imposed by the task. Thus, even though the adverse effects of aging may selectively target the frontal lobes, functional neuroimaging evidence indicates, paradoxically, that age-related over-recruitment of frontal networks can be beneficial (Angel, Fay, Bouazzaoui, & Isingrini, 2011; Peelle, Chandrasekaran, Powers, Smith, & Grossman, 2013).

Some insight into the mechanisms underlying over-recruitment of PFC comes from studies that have varied task demands to determine the level of demand at which overactivation is evident in older adults, and to ask whether there might be some level of demand at which younger adults also begin to activate these additional regions. Several studies that varied working memory load in either an n-back task or an item recognition task demonstrate that older adults recruit additional regions of dorsolateral PFC at low to intermediate memory loads, whereas younger adults bring these areas on-line only at higher loads (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Mattay et al., 2006; Schneider-Garces et al., 2010). Vallesi, McIntosh, and Stuss (2011) demonstrated this demand-related compensatory activation by varying the difficulty of a Go/No-Go task (low conflict versus high conflict), as well as by

assessing performance on the first block of trials, while the task was still novel, versus performance on the second block of trials, after participants had been accustomed to the task with practice. Compared to younger adults, older adults over-recruited a fronto-parietal network during the highest task demand (i.e., during high-conflict trials in the first block). Furthermore, this additional recruitment of supplemental brain regions was associated with a lower error rate, providing yet another indicator that additional fronto-parietal engagement was compensatory.

However, greater neural recruitment is not always associated with better task performance. Individuals who show more activation also can have worse behavior. For example, older adults with greater activation of the superior frontal gyrus had lower hit rates and lengthened response times when performing a visual selective attention task (Solbakk et al., 2008). This inverse association between activation and performance may be due to the level of task difficulty. Although greater neural recruitment can be beneficial at lower levels of task demand, as demand increases available neural resources may be insufficient to support the computational requirements of the task. These ideas relating task demand to age difference in activation have been summarized in the compensation-related utilization of neural circuits hypothesis or CRUNCH proposed by Reuter-Lorenz and Cappell (2008).

Cross-sectional evidence also suggests that older adults engage control processes differently than young adults, with greater emphasis on reactive control, which is engaged at later stages of information processing, than proactive control, which can be considered more preparatory in nature. For example, while completing demanding control tasks, older adults show a late-stage over-recruitment of frontal regions, which may reflect a strategy shift that results in preserved, but slower and more rigid task performance (Velanova, Lustig, Jacoby, &

Buckner, 2007). This so-called early-to-late shift (ELSA) of executive control strategies is also evident in the delayed functional connectivity of PFC and subcortical structures associated with memory (e.g., hippocampus), which may have important implications for maintenance of goals (Dew, Buchler, Dobbins, & Cabeza, 2012). Evidence from event-related potentials likewise suggests that older adults under-recruit control processes in response to a preparatory cue, but over-recruit in response to the target stimulus itself, thereby maintaining accurate performance, but at the expense of response speed (Kopp et al., 2014).

The importance of EF for maintaining cognition and effective performance more generally is evident in purely behavioral studies as well. Despite exhibiting age-related declines in executive functioning compared to their younger counterparts, those older adults who maintain higher levels of EF exhibit better behavioral performance. For instance, de Frias et al. (2009) found that better executive functioning was related to higher initial cognitive function and greater stability in cognitive function after a 3-year longitudinal assessment. Moreover, Chang et al. (2010) examined individual differences in EF and grouped individuals with mild cognitive impairment (MCI) into subsets of high and low performers based on Backward Digit Span and the Trail Making Test. MCI patients with higher executive functioning exhibited better performance on the Rey Auditory Verbal Learning Test, demonstrating the compensatory role preserved EF can play. In the same sample, Chang et al. (2010) further documented that prefrontal cortical thickness independently contributed to improved memory, above and beyond the medial temporal regions known to contribute to episodic memory.

Thus, collectively, data from cognitive-behavioral approaches and functional imaging methods demonstrate that individual differences in both behavioral and neural correlates

III. BEHAVIORAL PROCESSES

of EF can be related to effective cognitive performance more broadly. Based on these data, efficient use of existing and supplemental executive abilities has become an important facet of models of cognitive aging, and the PFC often plays a key role in such compensation. The Scaffolding Theory of Aging and Cognition (STAC) model proposes that compensatory scaffolding in the form of supplemental neural recruitment, neurogenesis, or enhanced neural connectivity, for instance, can help overcome the neural challenges and functional deterioration associated with age-related biological and environmental risk factors such as genetics, stress, and vascular impairments (Park & Reuter-Lorenz, 2009). Moreover, Stern's (2009) cognitive reserve account similarly posits that those with higher protective factors experience less pronounced age-related cognitive decline. Many of these protective factors are associated with greater neural health and well-developed executive abilities, including higher IQ, more years of education, and higher occupational attainment (see also Tucker & Stern, 2011). These models of cognitive aging reflect the fact that differences exist in the way that individuals experience and respond to cognitive aging, and, notably, they are particularly informed by experimental evidence implicating prefrontal and executive compensatory processes. Individuals who maintain higher levels of executive functioning, and those who are able to recruit supplemental prefrontal neural networks to cope with increasing task demands, tend to fare better.

Given the importance of executive functioning to successful performance of everyday activities, any significant declines in EF will likely negatively impact daily life, regardless of whether EF shows a unique or disproportionate age-related decline. Sakai et al. (2012) found that older adults with lower executive abilities reported a higher frequency of driving errors, both nonhazardous (e.g., entering the incorrect lane in a roundabout) and hazardous

(e.g., failing to notice pedestrians crossing the street). And, in this sample, reduced EF was also associated with declines in frontal gray matter. Moreover, Farias et al. (2009) found that longitudinal declines in EF predicted completion of daily activities independently from memory decline. Examples of daily activities that were tracked in this study include navigation on familiar streets, performance of household duties, and handling money, among others. Finally, using structural equation modeling, Vaughan and Giovanello (2010) report that a latent executive component was significantly related to performance of activities of daily living, and that, in isolation, task switching was the best predictor. From these studies it is clear that executive capabilities are important to maintain independence in daily life and that declines in EF have measureable everyday consequences.

EFs, THE FRONTAL LOBES, AND LIFELONG AGING

From the various lines of evidence reviewed in this chapter, it is apparent that prefrontal cortex and EFs play a central and complex role in neurocognitive aging, being adversely affected on the one hand, and a source of potential support and maintenance of effective cognitive and behavioral functioning on the other hand. Brain-based studies appear to be more sensitive than behavioral measures to selective and early decline of frontal cortex, while also revealing increased reliance on the functions they mediate in older adults. As noted, the inconsistency of behavioral measures may stem from shortcomings of the measures themselves, in addition to the challenge of defining EFs and isolating the contexts in which they are most likely to emerge.

To the extent that EFs and the prefrontal networks on which they depend provide a source of support and compensation in later years,

it is essential to understand the lifelong processes that may bolster and expand the potential for executive compensation in later life. Longitudinal studies that document the trajectory of EFs from childhood through midlife and into old age are virtually nonexistent. The only lifespan functional imaging study to date suggests, by means of cross-sectional comparisons, that middle age is a point on a continuum that is intermediary between young adulthood and older age, and that overactivation of prefrontal and other cortical loci is evident by middle age (Kennedy et al., 2014). The potential longitudinal benefits of recruiting additional prefrontal sites are largely unknown. While it may be most beneficial to maintain a "youth-like" brain activation pattern into older age (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012), there is also evidence that older adults who show higher levels of PFC and hippocampal activity sustain high levels of memory performance over a 20-year period (Pudas et al., 2013).

Indeed, understanding individual differences in trajectories of executive and prefrontal functioning may be key to understanding cognitive aging. In the STAC model proposed by Park and Reuter-Lorenz (2009) prefrontal networks are hypothesized to serve a fundamental role in scaffolding functions, whereby they provide additional computational support when primary brain networks, which mediate task performance in younger brains, become less efficient due to aging. Their revised model, STAC-R (Reuter-Lorenz & Park, 2014), takes a lifespan, longitudinal perspective, according to which neural resources can be depleted or enriched by a variety of protective and risk factors throughout development. In this model protective and risk factors affecting an individual throughout developmental time not only influence brain health and the extent that cognitive function is enhanced and maintained across the lifespan but also influence the potential for scaffolding and recruitment of additional resources as brain efficiency declines in old age.

In closing, we should briefly acknowledge the additional relevant frontiers pertaining to EF and aging that are beyond the scope of this chapter. These include the important intervention work being done to enhance and sustain EFs using fitness and cognitive training regimens, the potential benefits of bilingualism on EF in older age, as well as new research directions in decision making, emotional control, and mindfulness in the elderly. It remains to be seen whether the theoretical perspectives about frontal function and aging reviewed herein can ultimately embrace these and other new developments. And if they do fall short, we can only hope that fresh ideas and critical new insights will emerge to unify our understanding of EF and the aging mind.

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