Published in final edited form as:

Lang Linguist Compass. 2016 July ; 10(7): 314–334. doi:10.1111/lnc3.12199.

The neural language systems that support healthy aging: Integrating function, structure, and behavior

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Abstract

Although healthy aging is generally characterized by declines in both brain structure and function, there is variability in the extent to which these changes result in observable cognitive decline. Specific to language, age-related differences in language production are observed more frequently than in language comprehension, although both are associated with increased right prefrontal cortex activation in older adults. The current paper explores these differences in the language system, integrating them with theories of behavioral and neural cognitive aging. Overall, data indicate that frontal reorganization of the dorsal language stream in older adults benefits task performance during comprehension, but not always during production. We interpret these results in the CRUNCH framework (compensation-related utilization of neural circuits hypothesis), which suggests that differences in task and process difficulty may underlie older adults' ability to successfully adapt. That is, older adults may be able to neurally adapt to less difficult tasks (i.e., comprehension), but fail to do so successfully as difficulty increases (i.e., production). We hypothesize greater age-related differences in aspects of language that rely more heavily on the dorsal language stream (e.g., syntax and production) and that recruit general cognitive resources that rely on frontal regions (e.g., executive function, working memory, inhibition). Moreover, there should be a relative sparing of tasks that rely predominantly on ventral stream regions. These results are both consistent with patterns of age-related structural decline and retention and with varying levels of difficulty across comprehension and production. This neurocognitive framework for understanding age-related differences in the language system centers on the interaction between prefrontal cortex activation, structural integrity, and task difficulty.

Introduction

Recent research has sought to explicate the neural and behavioral effects of aging on language processing. Behavioral work has suggested that language comprehension is largely maintained with age, while language production often declines. Despite these differences in behavioral outcomes, many studies indicate that during language processing, older adults recruit brain regions that younger adults do not. The primary goal of the current paper is to review the existing literature on the neural systems that support language in older adults, and

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to provide a framework for interpreting age-related differences in the language system, which centers on the interaction between prefrontal cortical activation, structural integrity, and task difficulty.

To this end, we first provide a brief review of theoretical accounts of age-related behavioral differences in language. We then discuss models of age-related differences in brain structure and function, explain how these differences relate to our understanding of language systems in younger adults, and integrate these models with behavioral findings. Although a detailed account of linguistic processes themselves is beyond the scope of the current paper, excellent discussions of models of comprehension and production can be found elsewhere (Dell et al. 1997; Indefrey & Levelt 2004; MacDonald & Seidenberg 2006; Pickering & Garrod 2004; Pickering & Garrod 2013). We focus specifically on fMRI studies of comprehension and production, examining the linkage between behavioral performance and age-related differences in fMRI activation (see Wlotko et al. 2010: for a comprehensive review of age-related studies using electrophysiological techniques). Finally, we will conclude by interpreting patterns of age-related differences in activation within the context of the dual stream model of language processing and the CRUNCH model. With this review, we hope to provide a more complete understanding of how models of aging and language fit together.

Theoretical Models of Age-Related Differences in Behavior and Cognition

Here we briefly describe several accounts of age-related differences in cognition. This overview will help to contextualize the behavioral changes observed in studies of language processing described later. Behavioral changes in older adults have been attributed to four primary domains of cognitive decline: processing speed, inhibition, working memory, and transmission deficits.

The processing speed theory suggests that older adults experience significant cognitive slowing (Salthouse 1996). As such, cognitive operations cannot be executed efficiently, and the output of prior cognitive operations may not be kept available for a sufficient amount of time. Cognitive slowing may affect both working memory (Salthouse 1992) and fluid cognition, which incorporates elements of integrative reasoning, geometric analogies, and spatial reasoning (Salthouse 1993). In fact, when processing speed is controlled for, age-related variance in other measures of cognition, such as memory, is greatly reduced (Salthouse 1996). However, Sliwinski and Buschke (1999) suggest that although processing speed accounts for a significant portion of age-related variance in memory in cross-sectional studies, this relationship decreases significantly in longitudinal designs. More recent work has further clarified the influence of processing speed on cognitive aging. Specifically, processing speed has been implicated in age-related changes in spatial ability and memory, but not verbal ability (Finkel et al. 2007) which suggests that generalized slowing may influence general cognitive abilities that interact with language (e.g., working memory), but not core language processes themselves. Overall, current data suggest that although processing speed may contribute to some age-related differences in cognition, any single factor account is not sufficient to explain cognitive decline in older adults (for recent reviews see: Drag & Bieliauskas 2010).

Although processing speed may partially account for age-related declines in working memory, limitations in mental capacity itself may also contribute to cognitive decline. While overall memory span decreases with age, working memory span has shown the largest age effect (Bopp & Verhaeghen 2005). These results suggest that tasks involving the manipulation of information would be most negatively influenced by capacity limitations. For example, working memory performance has been implicated in age-related variance in spatial memory (Cherry & Park 1993), procedural assembly (Morrell & Park 1993), and speech recognition (Stine & Wingfield 1987). Capacity limitations may also underlie age-related deficits in sentence comprehension, particularly for longer sentences and those with more complex grammatical structures (Just & Carpenter 1992). This suggests that working memory, or more broadly, executive function, may affect language processing in older adults. Additional research supports this hypothesis, illustrating that increasing working memory demands in older adults resulted in slower speech rates (Kemper et al. 2003). More recently, working memory deficits have been tied to deficits in task or process coordination, a mechanism that could also explain age differences in attentional control (Hoyer & Verhaeghen 2006; Verhaeghen & Hoyer 2007).

The independent roles of processing speed and working memory in age-related declines in cognition may be difficult to disentangle. Previous research suggests that while processing speed may contribute to age-related variance across memory tasks in general, working memory plays a secondary and more specific role in difficult memory tasks (Park et al. 1996). Thus, while processing speed and working memory may not be completely independent domains (Verhaeghen & Salthouse 1997), they appear to differentially contribute to age-related cognitive changes.

The observed link between working memory and comprehension led to the development of a third theory: the inhibitory deficit theory (Hasher & Zacks 1988; Lustig et al. 2007). The inhibitory deficit theory suggests that older adults process more information than younger adults, and while at first glance this may seem beneficial, it may also serve to distract or otherwise impede completing the goal at hand (for a recent review see Healey et al. 2008). For example, an early study by Hamm and Hasher (1992) found that older adults were more likely than younger adults to accept alternative interpretations during a test of reading comprehension. A limited capacity theory would predict that older adults should keep fewer alternative interpretations active while reading, and similarly, a processing speed account would suggest that decay from slower processing may limit the number of alternatives that can be maintained. Previous studies suggest that age-related declines in inhibitory control may result in an *increase* of information entering working memory, even if this information is not necessary for task success (Hamm & Hasher 1992). Thus, such results are more consistent with the inhibitory deficit account of cognitive aging. Likewise, data suggest that inhibitory deficits may be independent of capacity limits, as they are observed in older adults during the recruitment of intentional control processes, regardless of the memory capacity required by the task (Collette et al. 2009; Hamm & Hasher 1992). The inhibitory deficit theory also suggests that age-related deficits in the ability to inhibit irrelevant information can affect attentional performance (Lustig et al. 2006), reading speed (Carlson et al. 1995; Connelly et al. 1991), memory (Collette et al. 2009), and pattern learning (Kramer et al. 1994), demonstrating that such a deficit may underlie changes a wide variety of cognitive

processes, including some aspects of language. However, recent memory research suggests that age-related inhibition deficits can be attenuated if participants are provided with a clear strategy for suppressing irrelevant information (Murray et al. 2015). These data indicate that older adults are not unable to recruit inhibitory processes, but they may experience increased difficulty initiating or generating strategies that lead to success (Murray et al. 2015). However, it is still untested whether performance in language tasks could be aided by providing such strategies.

Unlike the three previously mentioned theories that invoke a specific cognitive process to explain general age-related differences in behavior, the transmission deficit theory was specifically proposed to account for age-related differences in language. According to this theory, connections between nodes within semantic and phonological networks are weakened with age, reducing the degree to which one node can prime another (MacKay & Burke 1990). The extent to which these weakened connections affect behavior and cognition depends on the organization of the particular language system. Specifically, transmission deficits have been invoked to explain age-related changes in phonological aspects of language production (James & Burke 2000). The transmission deficit theory posits that the phonological system is most vulnerable to age related decline because of the lack of redundancy in the phonological and orthographic nodes (Burke & Shafto 2004). Similarly, this theory can also account for age-related difficulties in learning new associations, such as those between a face and a name (James et al. 2008). Because the nature of these associations is arbitrary and non-redundant, they are likely to be weakened with age. By contrast, age-related declines in semantic components of production and comprehension are not as apparent due to the highly redundant and inter-connected nature of the semantic system (Burke et al. 1991; James & Burke 2000; Laver & Burke 1993). This redundancy can effectively compensate for a single weak semantic connection, because it is likely that multiple, different connections can provide sufficient activation (Burke & Shafto 2004). Thus, unlike other accounts of cognitive aging, this theory makes predictions related specifically to the language system: transmission deficits will be more pronounced during tasks that emphasize phonological processing and transmission deficits will be more apparent in language production tasks, rather than in language comprehension tasks.¹

Age-related Differences in Brain Structure

In addition to age-related differences in behavior, structural brain changes across the lifespan have also been the subject of much research. Gray matter volume begins to decline as early as post-puberty (Giedd et al. 1999). On the other hand, white matter volume increases throughout adolescence, and begins to decline sometime after 30 years of age (Bartzokis et al. 2001; Bartzokis et al. 2004).

Two primary patterns of structural differences observed in older adults may help to explain age-related differences in language. The first pattern of decline unfolds in an anterior to posterior gradient. This pattern follows the theory of retrogenesis, which suggests that

¹Phonological aspects of reading comprehension are less susceptible to transmission deficits because among skilled readers the phonological code is readily available through orthography (Bonin et al. 2001).

regions that are among the last to develop and myelinate are among the first to show age-related decline. Developmental studies suggest that later developing regions include prefrontal cortex and left posterior temporal cortex (Sowell et al. 2003; Sowell et al. 2001). Consistent with these developmental patterns, the most prominent age-related declines in gray matter volume are frequently observed in frontal and parietal cortices (Good et al. 2001; Resnick et al. 2003), with frontal cortices exhibiting the greatest cortical thinning (Salat et al. 2004). Similar regional patterns of decline have been observed in white matter (for a review see Madden et al. 2012). This pattern of prefrontal decline suggests that aspects of language such as syntax and language production, which rely on the left inferior frontal gyrus (IFG), may be significantly affected by age. Because left IFG also supports executive function (Braver et al. 1997; Dove et al. 2000; Moss et al. 2005; Swick et al. 2008; Zhang et al. 2004), structural degradation of this region might significantly affect language tasks that involve high executive function demands. The general term “executive function” includes cognitive processes such as attention, inhibition, task switching, planning, and updating (Alvarez & Emory 2006; Miyake et al. 2000; Smith & Jonides 1999). Because these aspects of cognition may underlie general age-related behavioral differences, it is important to consider the intersection between general cognitive abilities that rely heavily on frontal cortex and language processes in aging.

The second pattern of structural decline observed in older adults follows a superior to inferior gradient, such that more superior tracts exhibit greater age-related decline than inferior tracts (Sullivan et al. 2010; Zahr et al. 2009). These differences are particularly relevant to studies of language and aging because superior white matter tracts (e.g., arcuate fasciculus and superior longitudinal fasciculus III) play a significant role in language functions, such as speech production and syntax (e.g., Maldonado et al. 2011; Stamatakis et al. 2011). Once again, this pattern of age-related structural decline suggests that older adults should experience more age-related deficits in language processes that rely on dorsal tracts (e.g., production, Hickok & Poeppel 2007).

Theoretical Models of Neural Differences in Aging and Cognition

In addition to differences in brain structure, functional differences in brain activity are also observed with increased age. With respect to age-related differences in cognition, two findings are commonly reported: 1) older adults often engage task-relevant regions to a lesser extent than younger adults (e.g., Cabeza et al. 1997; Park et al. 2004; Rizio & Dennis 2014) and 2) older adults typically engage more brain regions than younger adults, often exhibiting patterns of bilateral activation for tasks that elicit lateralized activation in younger adults (e.g., Logan et al. 2002). These changes have been well documented across many cognitive domains, such as memory retrieval (Cabeza et al. 1997), perception (Grady et al. 2000), inhibitory control (Langenecker & Nielson 2003), and language processing (e.g., Wierenga et al. 2008).

Converging evidence suggests that reduced functional activation within task-relevant regions reflects age-related changes in neural and vascular systems, resulting in decreased signal-to-noise ratio in the brain (Li et al. 2001; Rajah & D’Esposito 2005). However, increased recruitment of neural resources in older adults has been interpreted through the context of

multiple different models (e.g., compensation, dedifferentiation). Critically, the way in which age-related increases in neural activity are interpreted must be linked to the corresponding level of cognitive function or behavioral performance. When increases in activation occur in conjunction with improved or maintained behavioral performance (relative to younger adults), this activation is termed “compensatory” (e.g., Cabeza 2002; Li et al. 2001; Rajah & D’Esposito 2005). Specifically, it is hypothesized that additional regions are recruited to supplement and compensate for structural or functional declines in other core regions. In contrast, when increased brain activation corresponds with declines in behavioral performance, this reflects neural “dedifferentiation” (e.g., Cabeza 2002; Ghisletta & Lindenberger 2003; e.g., Park et al. 2004). That is, increased patterns of activation reflect a decline in the efficiency of the neural networks. Some have suggested that dedifferentiation arises from an age-related reduction in inter-hemispheric inhibition, such that deficits in the ability to inhibit right hemisphere activity decrease the efficiency of left hemisphere function (Fling et al. 2012; Fling et al. 2011; Ghisletta & Lindenberger 2003; e.g., Park et al. 2004).²

General task difficulty may also influence the relation between performance and brain activation. A hybrid model, the compensation-related utilization of neural circuits hypothesis (CRUNCH, Fling et al. 2012; Fling et al. 2011; Reuter-Lorenz & Cappell 2008) has been proposed to account for task difficulty. The CRUNCH model proposes an interaction between task difficulty and brain activation. At low levels of task difficulty, increased activation compensates for neural decline and reduced efficiency in older adults. As a result, increased activation initially corresponds to maintained behavioral performance. However, as task demands increase and begin to outstrip cognitive resources, brain activation plateaus or declines, and behavioral performance worsens. Thus, while increased brain activation in older adults can help maintain behavioral performance in certain situations (i.e., simple tasks of low difficulty), more difficult tasks require a degree of neural processing that is not available to older adults, and consequently, behavioral performance declines.

In addition to task difficulty, other factors may also influence the relationship between behavior and functional activation. Older adults tend to be more variable in both performance and patterns neural activation (CRUNCH, Garrett et al. 2011; MacDonald et al. 2006; Reuter-Lorenz & Cappell 2008). Thus, if a specific behavior is not correlated with neural activity, it may partially reflect increased variability in these measures. Moreover, fMRI studies often recruit smaller samples than traditional behavioral studies, which further hampers the detection of significant effects. As a result, small but important differences may be more difficult to detect in older adults. Taken together, neural models of aging (compensation, dedifferentiation, and CRUNCH), as well as factors such as variability and sample size, may be useful in interpreting age-related differences in the neural substrates that support language function.

²Although it may be tempting to draw parallels between this neural inhibition and the inhibitory deficit theory, it is still yet untested whether the two are related.

Interim Summary

Patterns of age-related decline appear to affect multiple cognitive processes, and several theories have been proposed to account for these differences (e.g., processing speed, inhibitory control, working memory, and transmission of priming). While the speed, inhibition, and working memory theories try to account for domain-general cognitive changes, only the transmission deficit theory makes specific predictions about language. From a structural standpoint, older adults typically experience declines in frontal and superior regions, with more posterior and inferior regions exhibiting significantly less decline. Based on these findings, one might predict more apparent age-related differences in language processes that rely on dorsal language regions, with relative sparing of tasks that rely on ventral language regions. Moreover, the pattern of age-related structural differences suggests that language functions that rely heavily on domain-general aspects of cognition that rely on frontal regions (e.g., executive function, working memory, inhibition) would be more susceptible to age-related decline. In the coming pages, we will provide evidence for these assertions, in addition to presenting an overview of the ways in which patterns of compensation and dedifferentiation are reflected across studies of age-related differences in the language processing system.

Comprehension

Age-related behavioral and cognitive differences in comprehension

Although increased age is typically characterized by some domain-general declines as well as some declines in language production, many language functions are well maintained throughout the lifespan. Specifically, older and younger adults tend to exhibit similar ability in language comprehension and semantic processing. For example, older adults have larger vocabularies than younger adults, and both groups display similar word associations (Alwin & McCammon 2001; Verhaeghen 2003). Both older and younger adults exhibit semantic priming effects (Bowles et al. 1983; Burke & Peters 1986). In addition, online measures suggest that spoken language comprehension remains intact as we age (Bowles 1989; Burke et al. 1987; Madden et al. 1993), especially at normal speech rates (Waters & Caplan 2005; Waters & Caplan 2001). Both older and younger adults benefit from literal (Wingfield et al. 2003) and figurative contexts (Newsome & Glucksberg 2002). In discourse processing, the ability to build and use situation models is preserved with age (Dijkstra et al. 2004; Radvansky et al. 2003; Radvansky et al. 2001). These findings indicate that many semantic aspects of comprehension change less with age (for comprehensive reviews of behavioral studies of language and aging see Burke & Shafto 2008; Wingfield & Stine-Morrow 2000).

Although the research generally supports the idea that language comprehension is robust against age-related decline, other data indicate that older adults do not use available predictive information in the same way as younger adults (Federmeier & Kutas 2005). Although this finding has been observed primarily with contextually rich sentences (i.e., strongly constrained sentences), these between-group differences may be linked to age-related deficits in working memory (Federmeier & Kutas 2005), suggesting that language tasks that place high demands on executive functioning might be particularly susceptible to age-related changes. On the other hand, previous research also suggests that older adults

may be *more* sensitive to contextual information than younger adults, because they are able to compensate for deficits in visual form recognition by relying on sentence context (Madden 1988). Older adults also construct situation models earlier than younger adults during reading tasks, which underscores their reliance on context (Stine-Morrow et al. 1996). Overall, these studies suggest that although older adults may be more dependent on context than younger adults during language processing, they may use contextual cues less efficiently during sentence comprehension, and are generally slower to make use of new information (e.g., Federmeier & Kutas 2005).

Age-related deficits have also been observed when comprehension is made more difficult by placing greater demands on the working memory system, such as when processing syntactically complex (Wingfield et al. 2006) or ambiguous sentences (Kemper et al. 2004), or when processing faster speech rates (Wingfield et al. 2003). Comprehension impairments in older adults may result from other, more secondary deficits, such as resource allocation. For example, Titone et al. (2000) reported that older adults fail to modify their behavior or strategy when information becomes increasingly difficult to comprehend. Taken together, these behavioral results indicate that while language comprehension is generally spared, comprehension tasks that place high demands on working memory capacity or resource allocation are especially vulnerable to age-related deficits. This is consistent with neuroimaging studies that have demonstrated greater structural decline in frontal regions that support working memory and executive function (Good et al. 2001; for a review see Madden et al. 2012; Resnick et al. 2003; Salat et al. 2004).

Age-related functional changes in comprehension

A nuanced analysis of the neural systems that support language in healthy aging requires a brief summary of how language is instantiated in younger adults. A typical perisylvian language network includes the inferior frontal gyrus (IFG), insula, superior temporal gyrus (STG), middle temporal gyrus (MTG), inferior temporal gyrus (ITG), and regions within the inferior parietal lobule (e.g., Hickok & Poeppel 2007; Indefrey & Levelt 2004; Price 2012). One prominent model of language comprehension, the dual stream model of speech processing, posits distinct dorsal and ventral neural pathways (Hickok & Poeppel 2007). The largely left-lateralized dorsal stream, which incorporates the IFG, premotor cortex, insula, and superior parietal-temporal cortex (Spt), integrates sensory and motor representations, and supports speech perception and production. The ventral stream, however, is more bilaterally distributed. This pathway, which includes the middle temporal gyrus (MTG) and inferior temporal sulcus, supports comprehension (Hickok & Poeppel 2007). The contribution of such ventral bilateral regions (i.e., MTG and inferior temporal gyrus) to semantic processing has been demonstrated through both lesion studies (e.g., Tyler et al. 1995; Wright et al. 2012) and visual object recognition tasks (e.g., Gerlach et al. 1999), suggesting that these regions are not necessarily modality-specific. In sum, whether or not a specific language process recruits bilateral or unilateral activation is largely dependent on the specific task requirements. In general, many language functions are left-lateralized. This is especially true for speech perception and production (Vigneau et al. 2011), as well as for more specialized language functions, such as syntactic processing (Bozic et al. 2010). However, bilateral activation has been shown to support aspects of language related to

semantic and early perceptual processing (e.g., Gerlach et al. 1999; e.g., Tyler et al. 1995; Wright et al. 2012).

With respect to aging, the neural correlates that underlie language processes display patterns of both age-related retention and decline, consistent with behavioral studies of language comprehension. Although the magnitude and extent of neural activation often differs across age groups, older and younger adults tend to engage some of the same brain regions during language comprehension tasks (for a recent review see Shafto & Tyler, 2014). For example, both younger and older adults engage the core left hemisphere language network (e.g., left IFG and left temporal regions) during semantic feature judgments (Peelle et al. 2013), semantic classification (Cho et al. 2012; Daselaar et al. 2003; Johnson et al. 2001), syntactic complexity manipulations (Tyler et al. 2010a), lexical decision tasks (LDT, Madden et al. 2002; Shafto et al. 2012), and word frequency manipulations (Madden et al. 1996). In addition, both older and younger adults exhibit priming-related reductions in functional activity in left IFG (Bergerbest et al. 2009; Daselaar et al. 2005; Gold et al. 2009; Lustig & Buckner 2004), left superior temporal gyrus (STG, Daselaar et al. 2005), and bilateral inferior temporal cortex (Gold et al. 2009).

Although older adults recruit core language regions during comprehension tasks, they often differ from young adults in the degree of left hemisphere lateralization. Although the ventral stream, which supports language comprehension, involves bilateral brain regions such as the middle temporal gyrus across the lifespan, older adults also recruit additional bilateral activation in regions not typically associated with language processing, such as the right inferior frontal gyrus (e.g., Peelle et al. 2013; Tyler et al. 2010a). As described previously, age-related increases in brain activation can reflect either compensation or reduced neural efficiency. Increased recruitment of bilateral regions reported in studies of language comprehension appears to support the compensation account (e.g., Meunier et al. 2014). For example, in a semantic feature matching task, high-performing older adults elicited greater activation in bilateral precentral gyri and left parietal cortex, compared to younger adults and low-performing older adults (Peelle et al. 2013). A study of sentence-level comprehension demonstrated that task accuracy for older adults was positively correlated with fMRI activation in right IFG and right insula (Peelle et al. 2010). Similarly, older adults who had similar behavioral performance to young adults elicited increased activation in right IFG in a word monitoring task in which syntactic complexity of auditory sentences was manipulated (Tyler et al. 2010a). A follow-up analysis of a subset of these original participants demonstrated that right IFG activation was positively correlated with gray matter atrophy in left hemisphere language regions, which suggests that increased right hemisphere recruitment served to compensate for structural decline in the left hemisphere. Together, these results suggest that neural reorganization - increased activation in regions not typically associated with language (e.g., in this case right prefrontal regions) - may serve to reduce the impact of age on language comprehension performance.

Of note, not all compensatory patterns of neural reorganization are associated with increased recruitment of *prefrontal* regions. Additional evidence suggests that recruitment of more posterior regions may also compensate for age-related decline in language-related regions during comprehension. In a lexical decision task in which all adults elicited lexical effects,

age-related differences in left IFG activation were not reported (Madden et al. 2002). Whiting et al. (2003) reported that older adults who were more sensitive to word frequency manipulations had larger PET activity changes in the left occipital-temporal pathway. Finally, in a study in which older and younger adults performed similarly on a lexical decision task, older adults demonstrated a greater functional sensitivity to imagability in left middle temporal gyrus (MTG, Shafto et al. 2012). These findings support the idea that compensatory-driven neural reorganization can occur during various comprehension-related tasks, and is not constrained to anterior regions.

Although the preceding results support compensatory neural reorganization (and by our definition, maintained or enhanced behavioral performance), other findings do not uphold this link. In particular, one notable study does not provide evidence for neural compensation. Johnson et al. (2001) reported that, despite similar levels of task performance, older adults displayed less activation than younger adults in left precentral gyrus during a semantic matching task, and less activation in right angular gyrus and left post central gyrus during a phonological matching task. These results indicate that reduced activation in regions that support language comprehension is not always accompanied by compensatory neural activity in other regions. As can be seen from the preceding descriptions, studies of language comprehension frequently report some degree of neural reorganization in older adults. While it is important to note the exceptions to this pattern, as well as the fact that both measures of behavioral performance and neural activity may be more variable in older than younger adults, in most instances, the recruitment of additional brain regions functions to support behavioral performance during a variety of language comprehension tasks.

Production

Age-related behavioral and cognitive changes in production

In contrast to the minimal impairment seen in aspects of language comprehension, language production is more susceptible to age-related decline. For example, older adults tend to have a reduced density of ideas when they speak and write, which may reflect age-related decreases in processing efficiency (Kemper et al. 2001; Kemper & Sumner 2001). In addition, when compared to younger adults, older adults generate more off-topic speech, which may be linked to an inability to inhibit irrelevant information (Arbuckle & Gold 1993; Arbuckle et al. 2000; Pushkar et al. 2000). Older adults also display deficits at the phonological level of production. For example, older adults have more slips of the tongue (MacKay & James 2004), and omit more phonemes from tongue twisters (Taylor & Burke 2000). They are also slower and less accurate when naming objects (for a review see, Mortensen et al. 2006), and have more pauses in their speech (Vousden & Maylor 2006). Compared to younger adults, older adults experience more tip-of-the-tongue states (TOTs), in which a target word or a person's name temporarily cannot be retrieved, although its meaning and semantic features are known (Burke et al. 1991). Age-related differences in TOTs are not consistent with the inhibitory deficit theory, but instead, are better accounted for by the transmission deficit theory (Burke et al. 1991). While the inhibitory deficit theory would suggest that TOT states result from an inability to suppress competing alternatives, current data suggest that with increasing age, TOT states are *less* likely to be accompanied

by persistent alternatives (Burke et al. 1991). Thus, the increased rate of TOT states in older adults, combined with the reduced frequency of persistent alternatives and the retrieval of less partial information, is better explained by the weakening of connections between phonological and lexical nodes. Moreover, low frequency words produce more TOT states than high frequency words (Burke et al. 1991), though repetition priming appears to decrease TOT states for both younger and older adults (James & Burke 2000). Because older adults generally have larger vocabularies than younger adults (Park et al. 2002), each individual word may be used less frequently, which would also contribute to increased TOT states, and is consistent with the predictions made by the transmission deficit theory. However, the increased frequency of TOTs in older adults may also be partially related to age-related slowing in processing speed. According to Kail and Salthouse (1994), decay may begin to affect the outcome of processing stages if processing extends over a long period of time (as might be the case with older adults). With respect to TOT states, if priming is slowed with age, activation of any given lexical or phonological node may begin to decay by the time the next node is primed, effectively decreasing word retrieval success, though this has not been explicitly tested experimentally. Overall, while processing speed and inhibitory control may contribute to the observed patterns of data, evidence suggests that the TDT best explains age-related differences in language production.

Age-related functional changes in production—As previously mentioned, the dual stream model of speech processing proposes two neural pathways, with the more left-lateralized dorsal stream (including IFG, premotor cortex, insula, and sPT), supporting language production (Hickok & Poeppel 2007). For example, using functional and structural MRI in younger adults, Saur et al. (2008) demonstrated that regions within the dorsal pathway, specifically the superior temporal and frontal/premotor regions, were functionally associated with speech repetition, as measured by repeated aural presentations of words and pseudo words (Saur et al. 2008). There is also evidence that syntactic processing is supported primarily by the dorsal pathway (Friederici 2009). However, others maintain that complex operations, such as syntactic and morphological processing, may recruit *both* dorsal and ventral pathways as a synergistic system (Rolheiser et al. 2011).

Like language comprehension, language production also appears to recruit left IFG, regardless of age. Recruitment of this region in older adults has been observed during semantic (Meinzer et al. 2009; Meinzer et al. 2012b) and phonological verbal fluency tasks (Meinzer et al. 2009), successful naming and TOT states (Shafto et al. 2010), and covert categorical word generation tasks (Destrieux et al. 2012). Together, these results demonstrate that at least one core language region of the left-lateralized dorsal stream continues to play a critical role in language production for healthy older adults.

A compensatory account of cognitive aging has been applied to specific instances of language production, but results are generally less consistent with this explanation. Illustrating such a pattern of compensation, older adults who matched younger adults in task performance exhibited greater activation in right prefrontal cortex during object naming (Wierenga et al. 2008) and verb generation (Persson et al. 2004), following the general pattern observed for comprehension tasks. Similar results have been reported for semantic verbal fluency tasks, but only with a group of participants who ranged in age from 22 to 56

(Nagels et al. 2012), leaving it unclear whether a similar pattern would be observed for adults 60 years of age or older. Lastly, Soros et al. (2011) also observed increased prefrontal activation for older adults during a syllable production task, despite no age-related difference in behavior. However, this particular task required none of the components of lexical selection that are typically present in studies of language production. Moreover, task success (which required participants to repeat syllables that had been auditorily presented) did not rely heavily on internally driven processes or strategies. As such, these results may provide preliminary evidence for the CRUNCH model, which predicts that compensatory activity should be observed in association with lower task demands. Although these findings suggest that age-related increases in right prefrontal activity may facilitate or maintain language production abilities during certain tasks, support for a compensatory model is most apparent for production tasks that are least demanding.

In contrast to the preceding studies, other data from production tasks better fit a dedifferentiation model. Two previous studies have reported increased right IFG and middle frontal gyrus (MFG) activity for older adults during semantic fluency tasks, when compared to younger adults (Meinzer et al. 2009; Meinzer et al. 2012b). Critically, increased right frontal activity was negatively correlated with behavioral performance in older adults. In other words, increased activity in this region was associated with the production of fewer correct responses. These results are compatible with a dedifferentiation account of aging, which posits that activation of the right hemisphere in older adults during tasks that typically recruit left-lateralized activation may be indicative of reduced efficiency of the language production network. Moreover, such findings suggest that the age of the participants may drive the compensatory pattern of results (Nagels et al. 2012), as the two studies which examined verbal fluency in an older group of participants reported patterns of neural activation consistent with dedifferentiation. In addition, Diaz et al. (2014) reported that older adults recruited several brain regions to a greater extent than younger adults during phonological and semantic judgment tasks. In this study, however, only younger adults exhibited significant correlations between fMRI activation and behavioral performance. These results again suggest that increased activation in older adults did not support performance on either task, which is consistent with a dedifferentiation model of aging.

Geva et al. (2012) reported significantly greater activation in right IFG in older adults, as compared to younger adults, during a rhyme judgment task but observed no age-related differences in behavior. Interestingly, in both age groups, increased right IFG activation during correct trials was positively correlated with error rate. The authors suggest that this correlation reflects the involvement of right IFG in error suppression. However, it is also conceivable that the most error prone individuals recruit right hemisphere resources, which suggests that recruitment of this region may not be beneficial at any age. Thus, while older adults as a group did not perform significantly worse than younger adults, these results provide additional tentative evidence that during language production, the right IFG does not contribute to successful behavior in the same way it does during language comprehension.

Other findings of increased neural activity in older adults are not compatible with either the compensation or dedifferentiation model. Shafto et al. (2010) reported a negative correlation between TOT rate and functional activity in left and right insula for older adults only, such

that those older adults with higher levels of fMRI activation experienced the fewest TOTs (Shafto et al. 2010). However, older adults did not exhibit significantly greater activation than younger adults in these regions, and right insula activity was not related to measures of gray matter integrity (Shafto et al. 2010). These findings, inconsistent with accounts of compensation and dedifferentiation, illustrate the challenges associated with synthesizing the wide variety of reported activation patterns.

Few experiments include task difficulty as a variable through which functional data can be interpreted. However, this measure may help to better contextualize data within the framework of existing models of aging. In a study of semantic fluency, activity in the bilateral inferior frontal gyrus was positively correlated with task difficulty in both younger and older adults. However, because this activity was negatively correlated with behavioral performance, these data are not compatible with a compensatory model of aging, as the increased IFG activity was not associated with increased behavioral performance (Meinzer et al. 2012a). These results may be more consistent with the CRUNCH model, as increases in frontal activity were not beneficial when task demands were high. Also taking into account task difficulty, Persson et al. (2007) used a verb generation task to examine age-related differences in the posterior cingulate, a key region within the default mode network. Their results suggest that at low levels of task difficulty, younger and older adults show similar abilities to deactivate task-irrelevant brain regions. However, as task difficulty increases older adults experience more difficulty than younger adults in down-regulating these regions (Persson et al. 2007). Together, these two studies illustrate the importance of taking into account task difficulty when reconciling patterns of brain activity and behavior. Specifically, they both suggest that at higher levels of task difficulty, older adults may exhibit increases in brain activity that are not actually supporting their performance on production tasks.

Reorganization of the neural language systems in aging: Integration of the dual stream model of language processing and aging

As already discussed, previous research regarding the dual stream model of language has suggested that the dorsal stream, unlike the ventral stream, is left-lateralized in nature (Hickok & Poeppel 2007). Although some aspects of language processing are strongly left lateralized, emerging data suggests that with age, the right IFG is more frequently recruited, resulting in an increasingly bilateral dorsal stream (e.g., Tyler et al. 2010a; Wierenga et al. 2008). Several studies have reported age-related increases in activation that are specific to the right IFG (i.e. no age-related increases were seen in other regions, Bergerbest et al. 2009; Geva et al. 2012; Nagels et al. 2012; Persson et al. 2004; Tyler et al. 2010a; Wong et al. 2009). Thus, age-related changes to the language system involve reorganization of the dorsal stream such that there is more bilateral activation of frontal regions, which are most sensitive to age-related decline. Reorganization of the dorsal stream, but not the ventral stream, is most likely a product of these patterns of general age-related structural decline. Moreover, this reorganization parallels many of the changes that are observed with other aspects of cognition that have been theorized to underlie age-related behavioral changes. Increased recruitment of prefrontal regions in older adults also occurs during inhibition and working memory tasks (e.g., Grady et al. 1998; Grossman et al. 2002; Nielson et al. 2002), providing

a clear link between age-related differences in language and other higher-level cognitive tasks.

In line with these functional differences in the dorsal stream, inter-hemispheric white matter tracts may also be critical to functional reorganization in older adults, as these connections would support bilaterally distributed frontal activation. Such inter-hemispheric tracts may explain why older adults are more likely to recruit homologous regions of the frontal cortex rather than posterior cortical regions. The genu of the corpus callosum is a major pathway connecting bilateral frontal regions. Davis et al. (2012) found that structural connectivity between bilateral frontal regions was positively correlated with accuracy on a semantic matching task in older adults (Davis et al. 2012), suggesting that the maintenance of connections between the frontal lobe are particularly important for older adults, even though these frontal white matter connections are most sensitive to age-related decline.

Overall, the current literature indicates that age-related differences in the dorsal stream are most strongly characterized by increases in activity to the prefrontal cortex. Increased right-hemisphere activity in older adults does not suggest that these regions are completely spared with age. Although anatomical deterioration occurs bilaterally, increased right hemisphere activity may still partially compensate for functional and structural decline, particularly when task demands are relatively low. Importantly, these differences mirror that of other aspects of cognition, particularly those related to executive function. As we have seen in previous sections, the left IFG cannot be fully replaced by right hemispheric activation. In some instances, such as during language comprehension, right hemisphere activity may supplement dorsal stream function. In other instances however, such as during language production, increased activation may not aid behavior. Lastly, age-related differences in ventral stream activations are not observed as frequently, perhaps because these regions undergo less structural decline, obviating the need for reorganization.

A Neurocognitive Framework of Language in the Aging Brain

Based on the preceding review, it is clear that significant progress has been made in elucidating the neural systems that underlie age-related differences in language processes. However, a framework that provides a more comprehensive understanding of the intersection between theories of cognitive aging and language is still needed. There is considerable evidence that many language functions are maintained as we age, while others undergo noticeable decline. In some cases, research suggests that neural reorganization may help maintain normal language function, while in other cases differences in activation patterns are associated with behavioral decline. The most prominent feature of this reorganization process is increased bilateral activation, particularly across regions that correspond to the dorsal stream. In previous sections we characterized the nature of this change, illustrating that across both comprehension and production, older adults exhibit increases in fMRI activation, particularly in the right frontal cortex. We believe that achieving a better understanding of the nuances that underlie these patterns is the key to developing a novel neurocognitive model.

For many studies of language comprehension, differences in prefrontal cortex activation are related to compensatory processes. Only Johnson et al. (2001) has reported reduced

prefrontal activation for older adults compared to younger adults in a comprehension-based task, but these differences were relatively minor, as they did not meet the corrected statistical threshold used for other contrasts of interest. On the other hand, many of the language production studies provide evidence for dedifferentiation (but see also Wierenga et al., 2008 and Shafto et al., 2010). Specifically, increases in prefrontal cortex activity during production tasks generally do not appear to support behavioral performance. As might be expected, this pattern is not observed in *every* reported study, and there are certainly results that suggest a more nuanced interpretation is needed. For example, a compensatory pattern of results was observed during syllable production (Soros et al. 2011). The task, however, involved only repeating sounds, and thus was a relatively simple production task, which highlights the importance of considering task difficulty when evaluating the literature on this topic.

Considering the aforementioned information, we propose that changes to the language processing system can be best interpreted through the CRUNCH model (compensation-related utilization of neural circuits hypothesis Reuter-Lorenz & Cappell 2008). According to CRUNCH, patterns of brain activity may appear compensatory in nature at low levels of task difficulty, but when task demands increase, increased activation is no longer associated with maintained or improved behavior, and evidence for dedifferentiation emerges.

This framework provides a mechanism through which we can explain age-related neural changes in language. Specifically, comprehension, which may be generally less demanding because it requires processing of the stimuli, but not explicit generation, is associated with compensatory patterns of activity. When tasks become more difficult (typically those that require some form of production), evidence for dedifferentiation emerges. Importantly, this pattern can also be integrated with current theories of aging and domain-general aspects of cognition. For example, some frameworks of language processing have proposed that executive functions are particularly important during language planning and production (MacDonald 2013). For example, speech planning, a necessary component of production, requires the use of short term memory processes, the alternation between executing updating the speech plan, and the deactivation of the memory trace for parts of the speech production plan that have already been accomplished (MacDonald 2013). These aspects of production require domain-general cognitive abilities that rely on frontal cortices, illustrating the intersection of domain-general and language-specific processes. As another example, older adults experience deficits in working memory (Bopp & Verhaeghen 2005), which may make it difficult to maintain multiple aspects of the speech production plan across a delay. Processing speed deficits may impair the speed with which the plan can be executed and updated, and inhibition deficits suggest that older adults would have specific impairments in deactivating the memory trace for outdated aspects of the production plan. While these theories can address some aspects of age-related decline that are observed in language, the transmission deficit theory makes additional specific predictions about language impairments (namely that connections between phonological, lexical, and semantic nodes are weakened, and that the phonological system should be disproportionately affected due to the limited redundancy of the system and the inaccessibility of the phonological code during language production). These transmission deficits, combined with additional domain-general changes and changes to the structural integrity of prefrontal cortex, may make older adults

particularly susceptible to deficits in specific types of language processing. In this way, it becomes evident that language production, which imposes very specific constraints on the cognitive system, is likely much more challenging for older adults than typical comprehension-based tasks (barring extreme situations such as the comprehension of unusually rapid speech or complex grammatical structures). Because production relies more heavily on many aspects of cognition that decline with age (e.g. working memory, executive function, it may be more affected by age than comprehension. Based on this premise, the CRUNCH model can provide a comprehensive explanation for the difference in brain-behavior relationships that have been observed across language production and comprehension. Specifically, age-related deficits in certain aspects of cognition (both domain-general and language specific) contribute to the difference in difficulty between language production tasks and language comprehension tasks. As such, neural reorganization can help compensate during comprehension, but not during production.

Moreover, this framework can help to reconcile inconsistent results from previous experiments. According to the CRUNCH model, production tasks that have particularly low demands (e.g. syllable repetition) should elicit patterns of compensation rather than dedifferentiation, which is exactly what was observed by Soros et al. (2011). Similarly, this framework would also suggest that manipulating task difficulty in a study of either comprehension or production should reveal compensation-related patterns at low levels of difficulty and dedifferentiation-related patterns at high levels of difficulty. Preliminary evidence in support of this theory is found in the results already reported by Persson et al. (2007), but it will be of particular importance to investigate the way in which direct manipulations to task difficulty influence the relationship between behavior and activity in the prefrontal cortex. Recent work has already begun to illustrate this relationship, as language comprehension, when combined with an additional linguistic task, relied on increased recruitment of dorsal frontal and parietal regions in younger adults, as compared to natural listening. Older adults performed equally well as younger adults, and did not exhibit any age-related differences in activation during natural listening. Critically, age-related increases in bilateral PFC activation were observed during language comprehension when an additional linguistic task was added, which was mediated by grey matter density in the PFC (Davis et al. 2014). These results highlight the importance of considering the influence of task difficulty when investigating age-related changes to language processing. Our framework, based on the CRUNCH model, would predict that at even higher levels of task difficulty, age-related increases in PFC activation might still be observed, even if behavioral performance declines.

Within this framework, one primary question still remains. Specifically, there is still uncertainty regarding the exact role of regions that exhibit age-related increases in activation. It is certainly possible that increased right hemisphere activity supports the same language-specific cognitive processes that are typically carried out by left-lateralized regions in younger adults. An alternative hypothesis is that the right lateralized activity reflects increased attentional or executive processes which may help to compensate for under-recruitment of left-lateralized language regions at low levels of task difficulty, but are nevertheless unable to support successful behavior on more demanding tasks. For example, select neuropsychological and neuroimaging studies (Tyler et al. 2011; Tyler et al. 2010b)

suggest that patients with damage to the left IFG do not retain intact syntactic functioning, even though right frontal and temporal regions were more engaged. These data would suggest that right frontal regions may support domain-general aspects of cognition rather than language-specific processes. Indeed, regions of the right prefrontal cortex have often been implicated in supporting executive function and attention (e.g. Kane & Engle 2002). In addition to increased right prefrontal activation, compensatory activity during comprehension tasks has been reported in regions outside the prefrontal cortex that may indeed support language-specific or perceptual processes (Shafto et al. 2012; Whiting et al. 2003). Together, these results suggest that compensatory-related recruitment may support a combination of processes, including both domain-general and language processes.

Conclusion

Language is not a unitary function, but is instead recruits many different processes that are maintained with increasing age (e.g. lexical, semantic, and syntactic processing), while also relying on domain-general skills that may undergo significant age-related decline (e.g., working memory, speed, executive function). An understanding of how the brain is able to retain certain language abilities despite declines in gray and white matter is still emerging. One possible compensatory strategy is the recruitment of right hemisphere activation in specific situations, such as when performing tasks of low difficulty. We suggest that one framework that may be helpful in interpreting the diversity of results is the CRUNCH model, which suggests that task difficulty is a critical factor that influences the pattern and function of the brain's response. Research studies that investigate the relationship between the brain, cognition, and behavior are critical to developing insight into how we might begin to remediate age-related decline.

Acknowledgments

This project was funded by NIA grant R01 AG034138 (MTD). We thank the staff and scientists at the Brain Imaging and Analysis Center for their support of this project, especially the center director Allen W. Song. We thank Anna Eppes for assistance with the references and feedback on various drafts.

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