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Age-related differences in resolving semantic and phonological competition during receptive language tasks

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ABSTRACT

Receptive language (e.g., reading) is largely preserved in the aging brain, and semantic processes in particular may continue to develop throughout the lifespan. We investigated the neural underpinnings of phonological and semantic retrieval in older and younger adults during receptive language tasks (rhyme and semantic similarity judgments). In particular, we were interested in the role of competition on language retrieval and varied the similarities between a cue, target, and distractor that were hypothesized to affect the mental process of competition. Behaviorally, all participants responded faster and more accurately during the rhyme task compared to the semantic task. Moreover, older adults demonstrated higher response accuracy than younger adults during the semantic task. Although there were no overall age-related differences in the neuroimaging results, an Age×Task interaction was found in left inferior frontal gyrus (IFG), with older adults producing greater activation than younger adults during the semantic condition. These results suggest that at lower levels of task difficulty, older and younger adults engaged similar neural networks that benefited behavioral performance. As task difficulty increased during the semantic task, older adults relied more heavily on largely left hemisphere language regions, as well as regions involved in perception and internal monitoring. Our results are consistent with the stability of language comprehension across the adult lifespan and illustrate how the preservation of semantic representations with aging may influence performance under conditions of increased task difficulty.

1. Introduction

Normal aging is characterized by significant declines in gray matter volume and white matter integrity across the brain, with the prefrontal cortex among the most vulnerable regions (Barrick et al., 2010; Good et al., 2001; Raz, 2005; Resnick et al., 2003; Salat et al., 2005; Sowell et al., 2003). Some cognitive functions also show age-related decline, such as memory, perception and executive control (e.g., Craik and Bialystok, 2006; Park et al., 2002), while other cognitive functions such as language comprehension are relatively spared (Burke and Shafto, 2008). The relation between age-related neural and cognitive decline, however, is complex and requires further investigation. With respect to language, some processes, such as basic syntactic parsing and language comprehension appear to be well preserved despite neural atrophy because of functional reorganization of the neural language system (Shafto and Tyler, 2014; Tyler et al., 2010; Wingfield and Grossman, 2006).

Moreover, core language processes interact with attentional control systems that may be affected by aging (e.g., Braver and West, 2008; Kramer and Madden, 2008), and as core language processes increase in complexity this may further increase demands on attentional control. For example, studies of comprehension of sentences of varying syntactic complexity found consistent left-hemisphere lateralization for older and younger adults, especially when task demands were minimized (Davis et al., 2014). However, when task-demands increased, age-related increases in functional activation in task-control regions were observed, suggesting that such age-related increases in activation that are commonly seen in many studies may be in response to task-demands as opposed to natural language comprehension (Davis et al., 2014). We investigate here the neural basis of semantic and phonological processes in young and older adults during language comprehension and how it is affected by variation in task demands for attentional processes.

Cognitive models postulate that word recognition involves activa-

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tion of multiple candidates that share sensory, phonological, or semantic properties with the auditory or visual input. Competition between candidates continues until the best-matching candidate is selected (Allopenna et al., 1998; Marslen-Wilson, 1987; McClelland and Elman, 1986; Norris, 1994). One critical brain region involved in such selection processes includes left inferior frontal gyrus (IFG). Some neural models propose that left IFG subserves language selection processes, but with distinct sub-regions involved in different processes, such as dorsal left IFG's (BA 44) involvement in processing sentential syntax and language production, and ventral region's (BA 47) involvement in semantic processing (Dapretto and Bookheimer, 1999; Friederici et al., 2000; Poldrack et al., 1999). Other models have argued that left IFG has a domain-general role in selecting among competing candidates (Humphreys and Gennari, 2014; January et al., 2009; Moss et al., 2005; Schnur et al., 2009; Thompson-Schill et al., 2005, 1997). A recent study in younger adults further suggests that right IFG may play a role similar to left IFG in resolving competition at the word level (Bozic et al., 2010). Bozic and colleagues investigated embedded phonological word stems (e.g. “clay, /klei/” within “claim, /kleim/”) as a source of lexical competition in spoken word recognition, and found that both left IFG and right IFG were activated similarly to solve lexical competition from embedded stems. In contrast, only left inferior frontal regions were engaged in higher-level syntactic competition processes. While these results demonstrate bilateral IFG involvement in language tasks, non-linguistic stimuli were not examined, so the specificity of IFG for language processes remains unresolved.

While left-lateralized regions, such as IFG and temporal cortex, have established roles supporting core language processes, the potential contribution of right hemisphere regions, particularly frontal cortex, is of special relevance to studies of aging. Age-related increases in right hemisphere activation are frequently observed (e.g., Cabeza et al., 2002), but there is considerable debate about whether these age-related neural differences reflect mechanisms of compensation (Cabeza et al., 2002; Park and Reuter-Lorenz, 2009; Peelle et al., 2010; Wierenga et al., 2008) or a more diffuse and less efficient neural response that is related to natural age-related decline of gray and white matter (Li et al., 2001; Park et al., 2004). Evidence in support of compensation includes reports of increased functional activation in right IFG associated with higher accuracy during picture naming for older adults (Wierenga et al., 2008). Other studies have reported increased activation in right inferior frontal regions (BA 45/47) for older adults during an auditory syntactic comprehension task where their performance was comparable to younger adults’ (Tyler et al., 2010). Moreover, this increased right IFG recruitment was related to gray matter loss in left IFG regions, suggesting that increases in right hemisphere activation are compensatory and may be a response to neuroanatomical changes in the left frontal regions. Such decreases in gray matter within the language network may lead to decreased connectivity within specific areas of the language network but increased functional connectivity overall (Meunier et al., 2013).

However, increased functional activation has not always been associated with better performance (Logan et al., 2002; Meinzer et al., 2009). In a semantic fluency task, Meinzer and colleagues found negative correlations between language production and neural activity in right IFG in older adults, suggesting that the increased involvement of right IFG in older adults did not contribute to better performance. Others have observed increases in right frontal activation for older adults performing word and picture rhyme judgment tasks when they had comparable performance to younger adults (Geva et al., 2012). However, in both groups there was a positive relation between error rate and activation in right frontal regions suggesting that the worst performers recruited right hemisphere resources more (Geva et al., 2012). Our own work has shown that older adults produced more errors than young adults in a phonological judgment task that required covert production of picture names, and although older adults elicited greater activation than younger adults, this was not related to behavioral performance (Diaz et al., 2014). Thus, it is clear that in some instances, recruitment of right hemisphere PFC regions aids language performance, while in other cases, it does not.

The relation between age-related neural differences and language processes is even more complex because normal aging may differentially affect specific language processes. For example, semantic aspects of receptive and productive language abilities are largely preserved: Semantic knowledge, as indexed by vocabulary, increases across the life span (Alwin and McCammon, 2001; Verhaeghen, 2003), and many studies have provided convergent evidence in support of preserved semantic function in older adults across various tasks, such as semantic priming (Madden et al., 1993), semantic judgment (Little et al., 2004), and word associations (Burke and Peters, 1986). Likewise, phonological processes are preserved during language comprehension, but there are notable age-related declines in language production, such as increased retrieval failures in producing spoken or written words (Burke and MacKay, 1997; MacKay and Abrams, 1998; MacKay et al., 1999; MacKay and James, 2004; Shafto and Tyler, 2014). During a tip-of-the-tongue (TOT) state in which individuals know they know a word corresponding to a meaning but cannot retrieve the word itself (Brown and McNeill, 1966), older adults show less activation in the left anterior insula compared to young adults. This is consistent with older adults having weaker phonological retrieval, especially during more challenging word retrieval states (Shafto et al., 2010). Older adults showed a negative correlation between TOT rates and activation in left insula, suggesting that while overall older adults elicited less left insula activation than younger adults, those older adults who could produce more activation had fewer phonological retrieval failures. Thus we may expect different brain-behavior relations depending on the aspect of language being examined (e.g., comprehension – compensation, phonological aspects of production – dedifferentiation).

While several previous studies have examined the effects of age on neural activation during language production (Bergerbest et al., 2009; Diaz et al., 2014; Geva et al., 2012; Meinzer et al., 2009; Nagels et al., 2012; Tyler et al., 2010), previous research has not investigated how the frontal control system functions during different types of lexical competition in normal aging. In this study we manipulated executive control demands in both phonological and semantic aspects of word comprehension to investigate brain mechanisms involved in resolving semantic and phonological competition. In the present study, participants were instructed to make rhyme and semantic similarity judgments about word triplets, and perceptual similarity judgments about dot clusters. Each trial consisted of three items (either words or dot clusters) displayed with one item (the cue) presented above two other items (the target and distractor) and participants judged which of these items was more similar to the cue. In the language tasks, we manipulated the phonological or semantic overlap between the cue and distractor and between the cue and target. We calculated a composite measure of selection demands based on ratings of the similarities of the cue and target and of the cue and distractor to yield a single measure of phonological or semantic competition. We also included a perceptual similarity judgment task as a baseline condition, in which spatial dot pattern similarity was manipulated between the cue and target and between the cue and distractor dot displays. Across the three tasks, we parametrically modulated selection demands by directly correlating the neural activity of each stimulus trial with the corresponding selection demands of the trial. This method provided a more fine-grained tool than canonical factorial contrasts to investigate these brain-behavior relationships.

We hypothesized that inasmuch as older adults are able to maintain their language systems through neural compensation, there would be a significant relation between behavioral performance and functional activation for a given condition. The likely pattern of age differences is either increased activation for older adults in a region that supports language in both younger and older adults (i.e., over-activation), or