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Language of the Aging Brain: Event-Related Potential Studies of Comprehension in Older Adults

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Abstract

Normal aging brings increased richness in knowledge and experience as well as declines in cognitive abilities. Event-related brain potential (ERP) studies of language comprehension corroborate findings showing that the structure and organization of semantic knowledge remains relatively stable with age. Highlighting the advantages of the temporal and functional specificity of ERPs, this survey focuses on age-related changes in higher-level processes required for the successful comprehension of meaning representations built from multiple words. Older adults rely on different neural pathways and cognitive processes during normal, everyday comprehension, including a shift away from the predictive use of sentential context, differential recruitment of neural resources, and reduced engagement of controlled processing. Within age groups, however, there are important individual differences that, for example, differentiate a subset of older adults whose processing patterns more closely resemble that of young adults, providing a window into cognitive skills and abilities that may mediate or moderate age-related declines.

1. Introduction

Our cultural adages tell us that with age and experience comes wisdom, and, indeed, empirical data show that healthy older adults often have richer vocabularies and augmented stores of world knowledge (Light 1992). However, aging also brings decline in both physical and psychological abilities: a sore back or more difficult climb up the stairs may be accompanied by decreased ability to remember a phone number or the grocery list, increased tip-of-the-tongue experiences, and a harder time focusing concentration on a particular task. These psychological facets of normal aging are likely to become more consequential as life expectancy continues to increase in the developed world and as medicine offers more solutions to the physical problems of aging. It is clear that research on cognitive aging is an imperative so that intellectual functioning can be correspondingly prolonged.

Language comprehension is a particularly critical skill for normal everyday life, and one that occupies a fairly unique position in cognitive aging research. As opposed to memory, executive function, and most other cognitive phenomena, important aspects of comprehension have been thought to be relatively protected against age-related degradation. Although certain language tasks become harder with age, especially when resources are heavily taxed, older adults report little change in their ability to engage in conversations, read novels or the newspaper, and use language in everyday situations (Light and Burke 1993). Behavioral evidence corroborates these subjective impressions, in that older adults and younger adults often show generally similar performance on comprehension-related tasks (Burke and Shafto 2008). Yet this stability is surprising in light of the myriad age-related cognitive and neural changes that have been documented, many of which are

required for the rapid, complex processes involved in language (Craik and Salthouse 2008). It seems likely, therefore, that across the lifespan comprehension goals may be successfully met via importantly different configurations of cognitive and neural resources.

In fact, recent evidence – particularly from measures of processing during on-line comprehension, such as electrophysiological brain activity collected as participants read or listen to language – reveals that aging is associated with both quantitative and qualitative changes in the processes used to comprehend language. Work using event-related brain potentials (ERPs), which provide functionally and temporally specific indices of cognitive processing, has shown that the organization of knowledge in what is generally referred to as 'semantic memory' does seem to be similar for younger and older adults and that basic aspects of word processing remain stable across the life span. However, there are important age-related – and individual – differences in how that word-related information is then used during on-line language processing. Delineating these processing differences is critical for building an understanding of how the aging brain makes the best use of available resources, skills, and knowledge to afford rapid and successful comprehension, thereby allowing older adults to gain information from the environment and communicate to build and maintain social ties. Our review focuses on ERP findings at the word, sentence, and discourse levels, and in late controlled processes involved in the online construction of message-level meaning from text or speech unfolding in real time. We conclude with a discussion of individual differences that modulate the changes that are seen at the group level.

2. Electrophysiology of Language and the Aging Brain

Language is fast, complex, and hierarchically constituted. Successful translation of the noisy, relatively arbitrary, and often ambiguous language stream into meaning requires equally rapid cognitive processing composed of sub-processes using multiple mechanisms at several interacting levels. Although the study of cognitive aging is a truly multidisciplinary endeavor that involves methodologies, data, and theorizing at levels ranging from genetics and cell biology to sociology, characteristics of ERPs have made this method particularly valuable for the study of language comprehension. ERPs directly reflect (some portion of) neural activity in the brain, as they consist of voltage deflections recorded at the scalp that are generated by the synchronous firing of cortical neurons associated with some type of internal or external stimulus or response – in the case of language, usually words (see Allison et al. 1986; Luck 2005; see also Kutas et al. 2006, 2007 for language-specific discussions of the ERP).

The neural activity is recorded in real time, so that the ERP provides a millisecond-level record of brain activity that is concurrent with cognitive processing, rather than occurring several hundreds of milliseconds downstream (as is true of behavioral measures as well as imaging methods, such as functional magnetic resonance imaging, that measure slower hemodynamic signals). This characteristic also affords the functional specificity of ERP 'components' – identifiable features of the waveform that are associated with particular cognitive and neural processes. For example, components in the first several hundred ms after stimulus onset index the analysis of perceptual features in primary and secondary cortical areas. The N400, a component that follows these sensory responses, has been associated with early aspects of meaning processing and is a particularly important measure for studies of language comprehension. The N400 is evoked by any potentially meaningful stimulus and is sensitive to a wide range of manipulations involving meaning (Federmeier and Laszlo 2009), but not to other language factors such as syntax. The amplitude (size) of the N400 reflects how well the eliciting word 'fits' with its prior con-

text, and a reduction in N400 amplitude is taken as an indication of ease of semantic processing, akin to a reduction in reaction time in behavioral studies (see Kutas and Federmeier 2000).

The characteristics of ERPs that make them so suitable for studying language also make them particularly useful for studying age-related changes in comprehension (see also King and Kutas 1995). It is clear that aging has differential effects on cognitive subprocesses, and ERPs provide specific indices that allow these effects to be examined independently but in tandem. For example, during a language processing task one can measure general slowing on sensory components, examine patterns of effects on semantic access as indexed by the N400, and determine to what extent older adults recruit later processes associated with explicit evaluation of the stimuli. These separable effects would be conflated with each other and with additional decision or memory-related processes when measured with downstream indices involving reaction times or accuracy scores. Although a wide variety of behavioral tasks (naming, word/nonword decisions, semantic/syntactic judgments, and measures of verbal memory, among others) have been used to make inferences about language comprehension processes, comprehension itself is an inherently internal process without a necessary or even typical behavioral outcome. As ERPs can be recorded without imposition of any additional behavioral response, many studies take the approach of eliminating tasks beyond reading or listening for comprehension to avoid contamination of naturalistic comprehension processes with task-related processes.

Because ERPs directly reflect neural activity, basic neuroanatomical and neurophysiological changes with age (for reviews see Grady 2008; Raz 2009; Davis et al. 2008; a complete discussion of the literature on neurobiological changes with age is beyond the scope of this article) would be expected to manifest as overall group differences, and a number of such changes have been documented. The amplitude of many ERP components, including the N400, becomes smaller with age (see, e.g., Kutas and Iragui 1998), although the functional significance of this difference is not clear. One possibility is that changes in brain morphology cause differences in the configuration of neuron assemblies (such changes may also affect the distribution of a component over the scalp; e.g., Fjell et al. 2005), such that sets of neural generators that were previously geometrically aligned and synchronously firing are no longer so in the aging brain. Another possibility, however, is that the timing of components across trials becomes more variable for older adults, resulting in activity that is 'smeared' over time. This highlights an ambiguity in interpreting amplitude changes in ERPs (and in any method that makes use of signal averaging): a smaller mean amplitude can result from a smaller amplitude on every trial with fixed latency, or an equivalent amplitude on every trial with variable latency (see Walhovd et al. 2008 for an approach to differentiating the two).

Advancing age is also associated with delays in the peak latency of components (which are less ambiguous to interpret than overall amplitude or distributional changes). Sensory components are sometimes found to be delayed on the order of 10–50 ms (Anderer et al. 1996; cf. Lindenberger and Baltes 1994), and delays on later components, such as the N400 (Kutas and Iragui 1998) or the P300 (Anderer et al. 1996; Polich 1996), a component associated with working memory, are often of even greater magnitude. However, component delays do not always follow a pattern of sustained or increasing slowing across the cognitive processing stream. For example, N400s to auditory words in normal connected speech have been found to show no age-related latency shifts (Federmeier et al. 2003), despite age-related delays on earlier, sensory components. The temporal sensitivity of ERPs thus allows not only an accurate

assessment of the fairly pervasive timing changes that accompany aging, but the opportunity to examine the relationship in these timing changes across different facets of cognitive processing.

3. Word-level Semantic Processing

As alluded to above, lexical-semantic knowledge and the organization of this information have been shown to be quite stable throughout adulthood. Older adults tend to generate similar word associates and category exemplars as do younger adults that are matched for verbal abilities (Howard 1980; Burke and Peters 1986). Access to this information, although often globally slower in older adults, also seems relatively unaffected by age, as evidenced by preserved behavioral (Verhaeghen and Cerella 2008) as well as electrophysiological priming effects. For example, older adults' N400 responses, like those of younger adults, are facilitated by lexical associative priming (Federmeier et al. 2003) and category and antonym relationships (Iragui et al. 1996; Federmeier et al. Forthcoming). Findings across methods thus suggest that the strength and organization of connections between words and from words to their meanings remain qualitatively similar with age.

A possible exception, however, comes from work examining the processing of words with multiple meanings. A number of behavioral studies have found evidence that, at least when task demands are minimized, older adults select meanings of ambiguous words in a manner similar to young adults (e.g., Balota and Duchek 1991; Balota et al. 1999). Recent ERP evidence, however, suggests that these similar behavioral patterns may arise from qualitatively different neural processing. Meyer and Federmeier (2007, Forthcoming) examined the contributions of the left and right cerebral hemispheres to the processing of ambiguous words in younger and older adults. To bias processing toward one hemisphere, homographs were presented in the left or right visual half-field (see Banich 2002 for a description of this technique), followed by a centrally presented target word that was either unrelated in meaning or related to either the more frequent (dominant) or less frequent (subordinate) meaning of the homograph. N400 priming patterns revealed that, for younger adults, both meanings were active in the left hemisphere (LH), with the dominant but not subordinate meaning additionally becoming active in the right hemisphere (RH). Older adults, however, showed LH activation of the dominant meaning but RH activation of the subordinate meaning. These results thus suggest an age-related shift of subordinate meaning activation from the LH to the RH, resulting, in older adults, in a division of labor, with each hemisphere focusing on a distinct meaning. Similar age-related increases in bilateral activation patterns have also been noted in the hemodynamic imaging literature for a wide range of cognitive processes (see reviews in Cabeza et al. 2002; Reuter-Lorenz et al. 2000), although their functional significance is still debated. As will be discussed in more detail, for language comprehension in particular, age-related shifts in hemispheric contributions are particularly notable for the processing of message-level meaning.

4. Building a Message-Level Representation

The ability to monitor processing as it unfolds during naturalistic tasks such as reading or listening for comprehension has made ERPs an especially useful tool for studying sentence (and discourse) processing, and it is at this level in particular that important, pervasive age-related differences have been noted. In one study, for example, younger and older adults listened to auditorily presented sentences that were either congruent or grammatical but nonsensical, and could contain a sentence-medial pair of associated words

or not (Federmeier et al. 2003). Thus, as in Van Petten (1993), effects of lexical association and sentential context could be examined independently (i.e., lexical association without sentential context in incongruous sentences, or sentential context without lexical association) or together (lexical association within congruent contexts) compared to the effects of neither. At the sentence-final word, both groups elicited a smaller N400 for congruous compared to nonsensical sentences, showing that all participants were comprehending the sentences, consistent with their high performance on the concurrent sense-judgment task. However, as in prior work (Woodward et al. 1993; Ford et al. 1996), the N400 effect of congruity was smaller for older adults, although the peak latency of the effect was not significantly different across age groups.

Effects at the critical sentence-medial words (the associated pairs or counterpart unassociated pairs within the two types of sentences) were measured in four 200-ms epochs (0–200, 200–400, 400–600, 600–800 ms) to assess when effects of lexical association and sentential context were apparent in the waveforms. These analyses revealed an early effect of lexical association (0–200 ms) that continued throughout the epoch and did not interact with age group. Sentence-level effects were also apparent by 200 ms for young adults, but were not significant until at least 400 ms for older adults (see also Schwartz et al. 2003). Thus, although younger and older adults responded similarly to lexical association, older adults displayed a qualitatively similar but substantially delayed response to sentential context. Gunter et al. (1992) came to similar conclusions using a slightly younger population, suggesting that declines in sentence-level comprehension begin by at least the fifth or sixth decade of life (see also Kutas and Iragui 1998).

Federmeier and Kutas (2005) further explored the use of message-level information by older adults by examining the impact of sentential constraint. Sentences were either strongly constraining with a predictable ending or were weakly constraining with an unpredictable ending (e.g., 'She was suddenly called back to New York and had to take a cab to the *airport*./She was glad she had brought a book because there was nothing to read at the *airport*.'). For both younger and older adults, strongly constrained, predictable endings elicited facilitated N400s compared to unexpected endings. However, this effect was significantly smaller and delayed for older adults as a group, with the age-related difference being driven by the response to the expected completions. In particular, there was no age-related delay on the peak of the N400 to the unexpected endings, and a multiple regression based on a battery of neuropsychological measures predicted the peak latency of the N400 effect, but not the latency of the component elicited by unexpected endings. Thus, the data from this study, using entirely plausible sentences with simple constructions, are consistent with the claim that older adults are not as able as younger adults to efficiently make use of rich sentential context information to facilitate word processing.

A new data set expands upon these findings by completing both strongly and weakly constraining sentence frames with either the most expected ending or an unexpected but plausible ending (Wlotko et al. 2008, Forthcoming). Replicating the prior work, facilitation for the strongly constrained expected endings (compared with both the strongly constrained unexpected endings and the weakly constrained expected endings) was smaller and delayed for older adults. Furthermore, as shown in Figure 1, the effect of expectancy in weakly constraining sentences (weakly constraining expected versus weakly constraining unexpected) was not reliable for older adults (as it is for younger adults; Federmeier et al. 2007). Thus, these findings are consistent with prior claims that the ability to effectively use strong sentential context information is compromised with age, and further reveal that older adults show little facilitation of word processing at all when sentence contexts are weak.

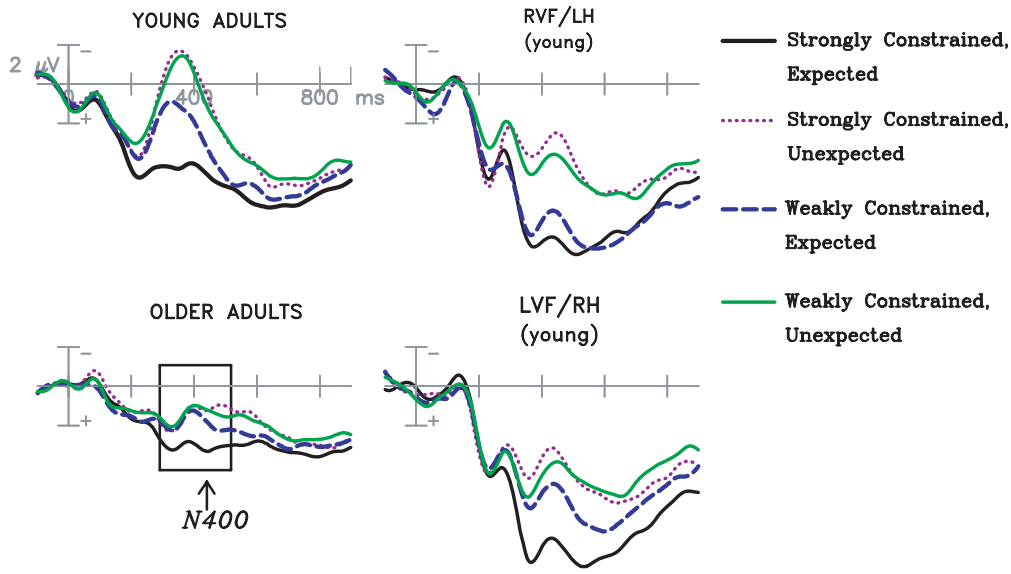

Fig 1. Older adults gain less facilitation from sentential context compared to young adults. When reading strongly or weakly constraining sentence frames completed by expected or unexpected endings ('He bought her a pearl necklace for her *birthday/collection*'. versus 'He looked worried because he might have broken his *arm/collection*'). Older adults showed no reliable difference in the N400 time window between weakly expected endings and the unexpected endings in the same sentence contexts, shown here at a middle parietal scalp site. This difference is also not significant for items presented to the right hemisphere (left visual field) for young adults, whereas the difference is exaggerated for left hemisphere (right visual field) processing. [Young adult data from Federmeier et al. 2007; RVF/LH and LVF/RH data from Wlotko and Federmeier 2007].

Overall, these studies show that when semantic information must be combined across words over time during sentence processing, older adults make less effective use of context information, resulting in reduced facilitation of strongly constrained expected words and eliminating facilitation for weakly expected words. Furthermore, facilitation, when it does occur, is substantially delayed. Delays of several hundred milliseconds are of great consequence when processing an input stream that typically comes at a rate of about 3–4 words per second. These changes, therefore, would seem to necessitate a concomitant shift in the neural and cognitive processes used by older adults to build the message-level meaning of a sentence or discourse.

Research on other kinds of processes needed to build a message-level representation has not been as well developed as in the use of semantic information during comprehension. However, King and Kutas (1995) show similar use of syntactic information by younger and older adults (modulated by working memory) and relate these findings to behavioral work (see, e.g., Kemper and Herman 2006). Similarly, Kemmer et al. (2004) observed that older adults showed no difference in the size or timing of the P600 response, an ERP effect sensitive to grammaticality. Thus, there are indications that syntactic processing may change less than semantic processing with age, although further research across a greater variety of syntactic processing contexts is needed.

5. Prediction in Comprehension

One way that sentential context can facilitate word processing is via predictive processing mechanisms, and ERP results attest to the pervasive use of predictive processing by young

adults, resulting in graded facilitation of semantic, lexical, morpho-syntatic, and even phonological and orthographic features of likely upcoming words (Federmeier and Kutas 1999b; Wicha et al. 2004; DeLong et al. 2005; Van Berkum et al. 2005; Federmeier et al. 2007; Laszlo and Federmeier 2009). In young adults, these mechanisms have been associated with LH language processing biases and are postulated to arise through the recruitment, during comprehension, of efficacious top–down pathways also used for language production (Federmeier 2007).

For example, Federmeier and Kutas (1999b) measured ERPs as young adults read for comprehension two-sentence contexts that could be completed by the most expected ending, an anomalous ending from the same semantic category, or an anomalous ending from a different semantic category. N400s were facilitated for the anomalous endings that shared features with the expected ending, and this facilitation was larger in strongly compared to weakly constraining sentence frames – i.e., in the case where the most expected completion was maximally predictable. This pattern shows that as sentence context accrues, semantic features of likely upcoming words become active, facilitating processing for those words, as well as related ones, when encountered. When the sentence endings were lateralized to one visual half-field (Federmeier and Kutas 1999a), only the LH showed this predictive processing pattern. In the RH, instead, expected endings were facilitated related to unexpected endings, but responses to the two types of anomalies did not differ.

The same conditions were examined for younger and older adults who listened to the materials from Federmeier and Kutas (1999a,b) presented as connected speech (Federmeier et al. 2002). Younger adults showed the same pattern for auditory as for visual presentation. In contrast, older adults showed a smaller facilitation for related anomalies, which was restricted to *weakly* constraining contexts – opposite of the pattern for younger adults. Thus, older adults (like the right hemisphere of younger adults) seem less likely to engage predictive processing mechanisms, or less effective at doing so, such that their processing is more driven by plausibility.

Prediction can provide benefits in comprehension by effectively 'pre-processing' information about likely upcoming words, thus saving resources when those words are actually encountered. However, predictions can also be wrong, entailing possible processing consequences. For young adults, Federmeier et al. (2007) found that these consequences manifested as changes in the size of a frontal positivity that followed the N400 (beginning around 600 ms post-stimulus onset), which was enhanced specifically for unexpected items in strongly constraining contexts. Although the functional specificity of this positivity remains to be fully understood, it seems to reflect a type of 'revision' needed when a prediction is not fulfilled. Thus, it is sensitive to constraint for unexpected endings (unlike the N400, which seems to reflect instead how well a word fits into its prior context; see also Kutas and Hillyard 1984), as a predictive processing strategy would entail.

However, data from Wlotko et al. (2008, Forthcoming), using the same materials as Federmeier et al. (2007) with older adult participants, show that older adults as a group do not elicit this positivity, as would be expected if the use of predictive mechanisms are not part of their comprehension strategies during sentence comprehension. With sentence processing paradigms, it is difficult to dissociate older adults' failure to engage predictive processing from the fact that, as already reviewed, they may have a more difficult time building a message-level meaning representation from which to make predictions. Therefore, Federmeier et al. (Forthcoming) examined age-related changes in predictive processing using category label cues ('A type of insect') followed, three-seconds later, by typical category targets, non-category incongruent targets, and atypical but congruent category

targets (e.g., 'ant/gate/hornet'). Younger adults elicited a late frontal positivity for the atypical but congruent category targets – very similar to the positivity from Federmeier et al. (2007) for unexpected but plausible sentence endings. Again, however, older adults as a group did not elicit this effect, showing that even in minimal contexts and with ample time, predictive processing becomes less likely with age.

Older adults thus seem less likely to predict during comprehension, making them less efficient at using sentence context information but also perhaps less affected by the processing consequences of revising incorrect predictions. The source of the decline in the use of predictive processing with age remains unclear. Federmeier (2007) postulated that predictive processing in comprehension arises largely from the LH, supported by the stronger top–down connections in the LH that would be required for efficient language production. Thus, one possible cause of the decline in predictive processing for older adults is the degradation of these feedback connections. Indeed, several data sets show a RH-like pattern for older adults in sentence comprehension studies (Wlotko et al. 2009b; see also Figure 1). Whether structural changes, perhaps in white matter tracts connecting frontal and temporal areas, can provide a locus of changes in comprehension with age is an important area open to investigation.

6. Multiple Meanings and Controlled Processes

Older adults' failure to recruit top–down predictive processing mechanisms during comprehension is an example of the more general trend for executive/controlled processes, as opposed to automatic processes, to be more affected by age (Hasher and Zacks 1988; West 1996; Foster et al. 1997; Craik and Anderson 1999; Hasher et al. 1999). Some have suggested that reductions in the use of controlled processes can arise from declines in sensory acuity that require more resources to be allocated to lower-level processing, leaving fewer resources available for higher-level operations (e.g., Wingfield, Tun, & McCoy, 2005; cf. Alain et al. 2004).

Within the domain of language, greater age differences have been found when cognitive capacities important for self-regulatory or executive functions are compromised with age (e.g., processing speed and inhibitory efficiency: Kwong See and Ryan 1995; or working memory: Norman et al. 1992; Van der Linden et al. 1999; see Stine-Morrow et al. 2006; for a review). Supporting ERP findings have been obtained from recent studies investigating ambiguity resolution (Lee and Federmeier 2009a) and meaning revision (Meyer and Federmeier Forthcoming), which both show that, with advancing age, top–down control mechanisms tend to become less available to shape meaning activation over time.

In Lee and Federmeier (2009a,b), for example, younger and older adults were asked to read noun/verb (NV), homographs (e.g., 'lobby'), and matched unambiguous words (e.g., 'month') that completed either congruent sentences with both coherent semantic and syntactic contextual information (e.g., 'You can usually find the registration desk of a hotel in the lobby') or syntactic prose sentences with grammatical syntactic structure but without coherent semantic information (e.g., 'You can usually install the math student of a day in the lobby'). Results from younger adults showed that, in comparison with unambiguous words, NV-homographs elicit (i) larger N400 responses in congruent sentences, indexing a semantic mismatch between the context and the automatic activation of the contextually inappropriate sense of the ambiguous word and (ii) a sustained frontal negativity in syntactic prose sentences, reflecting the recruitment of top–down mechanisms to aid semantic selection when semantic constraints are less available (Lee and

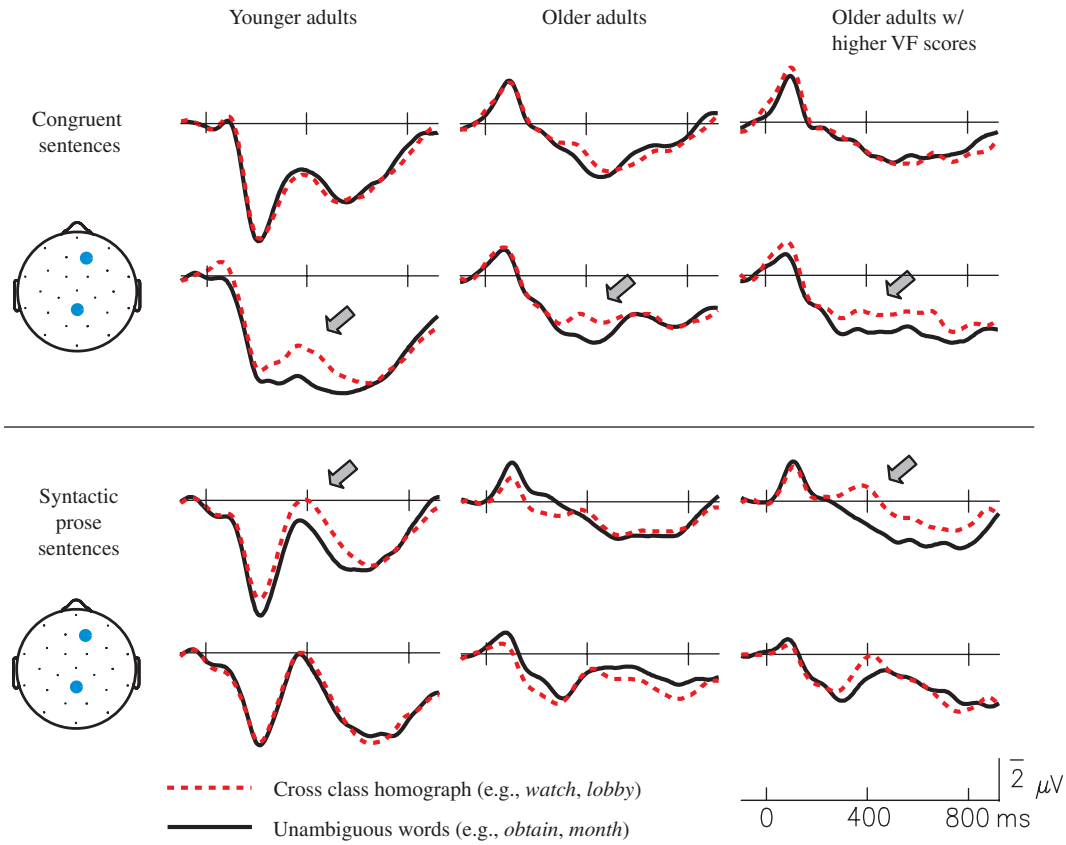

Fig 2. Grand average ERPs to ambiguous words (dashed line) and unambiguous words (solid line) are plotted separately for congruent sentences (upper panel) and syntactic prose sentences (lower panel) at two representative electrode sites (indicated by enlarged filled circles on the head diagrams). For younger adults (left column), the responses are more negative to the ambiguous words than to unambiguous words over central/posterior sites in the N400 time window (250–500 ms). In the syntactic prose sentences, however, the responses to ambiguous words are more negative than the response to unambiguous words over the frontal channels (200–700 ms). In older adults as a group (middle column), there were similar (although smaller) N400 effects for congruent sentences, whereas the frontal negativity previously observed in the syntactic prose condition in the young was absent. Only a subset of the older adults with higher verbal fluency (right column) showed the young-like frontal negativity effect.

Federmeier 2009b). Data from older adults, displayed in Figure 2, showed similar (albeit smaller) N400 effects for congruent sentences, suggesting that automatic semantic activation mechanisms are relatively well maintained. In contrast, the frontal negativity observed for the young in the syntactic prose condition was absent for the older adults, suggesting that the executive mechanisms involved in more difficult circumstances of ambiguity resolution have become less effective.

Thus, when semantic constraints are not available to aid meaning selection, younger adults recruit control processes, likely in frontal lobe regions (Badre et al. 2005; Zempleni et al. 2007), to aid with meaning selection. Older adults as a group, however, fail to do so, suggesting that they are less likely to efficiently and effectively select the meaning of ambiguous words in these circumstances. When semantic constraints are available, older adults, like younger ones, seem able to make use of that information to bias meaning selection, as seen in the N400 reductions observed in the congruent sentences of Lee and

Federmeier (2009a), as well as the patterns observed in the word priming study of Meyer and Federmeier (2007, Forthcoming). In those studies, the lateralized homographs and related or unrelated targets (already described) were preceded by either an unrelated context word or a context word that biased toward a meaning sense of the homograph different from the related target (e.g., 'river – bank – money'). Although N400 priming was observed in both groups for related targets (bank – money) when the context word was unrelated, when the context word biased meaning selection toward the homograph's alternate meaning, this N400 facilitation was absent for both groups. In other words, both groups seemed to use the context word to select one meaning of the homograph, such that words related to the other meaning were then treated similarly to wholly unrelated words. These findings are consistent with those of Swaab et al. (1998) and Taler et al. (2009), showing that older adults can use biasing context information to access the correct meaning of ambiguous words and words with metaphorical senses.

Although initial priming of the alternative meaning was blocked by prior meaning selection, young adults' ERPs (Meyer & Federmeier 2007) revealed that they are able to exploit control process to revise the interpretation at a later time, resulting in priming on the Late Positive Complex (LPC), a potential that follows the N400 and has been linked to explicit memory and semantic revision processes (e.g., Van Petten et al. 1991). Older adults as a group, however, failed to show LPC priming to related targets following a biasing context (Meyer and Federmeier Forthcoming). Thus, when initial meaning selection proves to be incorrect, older adults seem less effective than young adults at recruiting processing mechanisms to afford meaning revision (see also Wright and Newhoff 2002 and Titone et al. 2006). These types of changes in controlled processes may be related to what some have called 'risky reading' strategies (Rayner et al. 2006), or increased reliance on 'good enough' representations in comprehension (Christianson et al. 2006).

7. *Individual Differences in Comprehension*

The evidence reviewed here suggests that there can be more than one way to succeed in language comprehension: changes in neural and cognitive resources with age result in older adults relying on different processing pathways to effect comprehension (cf. Stine-Morrow et al. 2008b). Within both younger and older adults – but perhaps especially with age – there is also important individual variability in many of the cognitive abilities brought to bear on comprehension, which have been linked to specific kinds of differences in comprehension strategies. Whether these changes result strictly from differences in neural change with age, or in cognitive preferences or motivations (e. g. Carstensen et al. 2006), or a combination of several factors remains an important area of investigation.

In all studies, older adults have a reduced and delayed N400 effect of sentential context, consistent with their lower reading spans. In young adult populations, reading span (a measure of verbal working memory) is associated with the size of the N400 effect (Van Petten et al. 1997; Wlotko et al. 2009a). One explanation for this pattern is that a reduced working memory size means that sentence context information can be retained over smaller intervals, and, thus, is less likely to bear on the processing of upcoming words. The decline in working memory for older adults is sometimes offered as a cause of changes in comprehension (see King and Kutas 1995 and Burke and Shafto 2008 for discussions), and Federmeier and Kutas (2005) indeed found that reading span (along with verbal fluency) was a reliable predictor of the N400 constraint effect. However, working memory capacity alone can't explain all the findings, as sometimes young adults low on working memory span still differ from older adults – such as in their tendency to use

predictive processing mechanisms. A possible reason for this may be that in addition to the storage of contextual information, predictive processes also involve retrieval and generation of information relevant to the context.

Although older adults as a group show a decline in predictive processing, a subset of participants in these studies showed more young-like comprehension patterns. Across studies, the tendency for older adults to manifest predictive processing patterns in their ERP responses has been closely linked to verbal fluency (Federmeier et al. 2002, Forthcoming). Verbal fluency measures the efficacy and speed with which semantic and/or lexical information can be produced in response to a cue. In addition, it also requires many of the top–down processes required in prediction, such as the ability to generate and utilize effective retrieval strategies, monitor the verbal output to avoid repetition, and inhibit task-irrelevant semantic information. Older adults who are able to score well on a verbal fluency task may have less decline in top–down connections and thus be better able to engage predictive mechanisms. Similarly, in Lee and Federmeier (2009a), higher letter fluency was predictive of older adults showing young-like patterns of recruitment of controlled selection mechanisms, as indexed by the frontal negativity.

Finally, in addition to these findings at the sentence level, patterns of ERP effects at the word level have been linked to the ability to inhibit information, as measured by the Hayling test (Burgess and Shallice 1996). When word processing is relatively easy (e.g., retrieving the dominant meaning of a homograph), both younger and higher-functioning older adults – those with better inhibition and executive control – recruit both hemispheres, whereas lower-functioning older adults rely on the LH only. In contrast, when word processing is difficult (e.g., retrieving the subordinate meaning of a homograph), both younger and higher-functioning adults tend to recruit one specialized hemisphere, whereas the lower-functioning older adults then rely on both hemispheres. Thus, at the word processing level, inhibition seems to be important for allowing the selective recruitment of specialized resources that may be distributed across the hemispheres (cf. Banich 1998); other effects of inhibitory capacity have also been linked to sentence-level processing patterns in behavioral work (see Hasher and Zacks 1988; Zacks and Hasher 1997).

Collectively, these data support several types of explanations that have been offered as a basis for cognitive decline in aging (see Light 1988; Burke and Shafto 2008), but further show that there is likely no single cause. Instead, it seems that a combination of at least speed of processing, working memory resources, inhibitory mechanisms, and ability to recruit top–down control processes all contribute to the ability to efficiently access meaning information from words and to effectively make use of sentential context during online comprehension (cf. Kennedy and Raz 2009). The influence of these factors, however, is not global; instead, specific cognitive and neural resources seem to be related to the ability to maintain and update context information over time, use that information to anticipate predictive words, and recruit controlled processes to resolve ambiguity.

8. Conclusion

Aging brings a lifetime of experiences and knowledge that remain largely intact as the brain grows older. The evidence provided by electrophysiological investigations of language comprehension during aging shows that the organization and structure of semantic knowledge is similar across age, but when integrating meaning across words to form message-level representations, older adults show both quantitative and qualitative changes in processing. For example, effects of sentential context are delayed several hundred milliseconds for older adults – a striking amount considering the fast timescale of

comprehension. Yet older adults do build meanings from sentences, so the brain must compensate for the change in timing by adjusting resources and strategies. Some of these adjustments may be seen in the differences in controlled processing or a switch to a less predictive mode of comprehension for older adults. All of these changes are modulated by individual differences, highlighting the importance of understanding what types of abilities, strategies, or brain states may protect against some of the declines in comprehension seen in old age.

Although the research reviewed here provides a window into changes in online comprehension with age, future studies will further illuminate how older adults make use of other kinds of information to build message-level meaning (e.g., syntactic cues, common ground). Further, although findings have been consistent across auditory and visual modalities, this line of work would benefit from being more closely integrated with findings from more naturalistic settings, such as continuous rather than word-by-word reading – for example, as measured by eyetracking – or in situations with richer discourse and social contexts. Finally, enhanced links between cognitive changes and neurobiological ones will bolster understanding of the factors underlying these changes in online processing, be it changes in gray matter, white matter, neurotransmitter distribution, or a combination of these.

As one part of a multidisciplinary approach to investigating cognitive aging, we may hope that research of this kind could illuminate ways to stave off the most serious of the changes in cognitive ability. Other research has shown the importance of social interaction (Parisi et al. 2007; Stine-Morrow et al. 2008a,b) and physical fitness (Kramer and Erickson 2007; Hillman et al. 2008) on brain function. Thus, there are many ways we can ensure our minds and our bodies enable a rich and fulfilling life many decades after the brain begins to 'age'.

Short Biographies

Edward W. Wlotko is currently a Beckman Institute Postdoctoral Fellow at the University of Illinois. His research explores the individual contributions from and the cooperation of the two cerebral hemispheres in language comprehension, and how those contributions change with age. He received his Ph.D. from the University of Illinois at Urbana-Champaign in 2009.

Chia-lin Lee's research focuses on how different sources of contextual information are processed to shape the interpretation of individual words. Specifically, she is interested in how one-to-many mapping problems involved in lexical ambiguities are resolved in the brain and how relevant cognitive and neural mechanisms change in later adult life. Chia-lin Lee received a BA and an MA in Linguistics from National Taiwan Normal University and an MA in Psychology from the University of Illinois.

Kara Federmeier obtained her Ph.D. in Cognitive Science from the University of California, San Diego. She is currently an Associate Professor in the Department of Psychology at the University of Illinois, Urbana-Champaign and the director of the Cognition and Brain Lab, housed at the Beckman Institute for Advanced Science and Technology. Her NIH-funded research uses event-related potentials to examine brain mechanisms of meaning access and integration, including hemispheric differences in language comprehension, changes in language processing associated with normal aging, and the interplay of language and memory. In 2006, she received the Society for Psychophysiology's Award for Distinguished Early Career Contributions to Psychophysiology, and in 2010, she received the Cognitive Neuroscience Society's Young Investigator Award.

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