Neuropsychologia 117 (2018) 135–147

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Electrophysiological evidence for preserved primacy of lexical prediction in aging

Shruti Dave[a,b,*], Trevor A. Brothers[a,c], Matthew J. Traxler[a], Fernanda Ferreira[a], John M. Henderson[a], Tamara Y. Swaab[a]

[a] Department of Psychology and Center for Mind and Brain, University of California, Davis, USA
[b] Department of Medical Social Sciences, Feinberg School of Medicine, Northwestern University, USA
[c] Departments of Psychology and Psychiatry, Tufts University and Massachusetts General Hospital, USA

ARTICLE INFO

Keywords:
Prediction
Contextual Support
Aging
N250
N400
Post-N400 positivity
Reading

ABSTRACT

Young adults show consistent neural benefits of predictable contexts when processing upcoming words, but these benefits are less clear-cut in older adults. Here we disentangle the neural correlates of *prediction accuracy* and *contextual support* during word processing, in order to test current theories that suggest that neural mechanisms underlying predictive processing are specifically impaired in older adults. During a sentence comprehension task, older and younger readers were asked to predict passage-final words and report the accuracy of these predictions. Age-related reductions were observed for N250 and N400 effects of prediction accuracy, as well as for N400 effects of contextual support independent of prediction accuracy. Furthermore, temporal primacy of predictive processing (i.e., earlier facilitation for successful predictions) was preserved across the lifespan, suggesting that predictive mechanisms are unlikely to be uniquely impaired in older adults. In addition, older adults showed prediction effects on frontal post-N400 positivities (PNPs) that were similar in amplitude to PNPs in young adults. Previous research has shown correlations between verbal fluency and lexical prediction in older adult readers, suggesting that the production system may be linked to capacity for lexical prediction, especially in aging. The current study suggests that verbal fluency modulates PNP effects of contextual support, but not prediction accuracy. Taken together, our findings suggest that aging does not result in *specific* declines in lexical prediction.

1. Introduction

Current models of online language processing suggest that successful reading and listening comprehension rely on the active anticipation of upcoming information (e.g., Altmann and Mirković, 2009; Clark, 2013; Huettig, 2015; Kuperberg and Jaeger, 2016). According to these models, comprehenders use local contextual information, as well as general event and semantic knowledge, to pre-activate likely upcoming words before their presentation. When these predictions are confirmed, readers show neural and behavioral effects of facilitation, representing the successful pre-activation of relevant sensory and semantic features. Studies investigating these prediction mechanisms have primarily focused on the effect of cloze probability during reading, which is typically operationalized as the number of participants providing a particular sentence continuation in an offline production task (Taylor, 1953). When recording event-related potentials (ERPs), cloze probability has been shown to have a substantial effect on the neural responses triggered by individual words in context, with unpredictable words resulting in larger N400 amplitudes than items that are predictable given available context (e.g., DeLong et al., 2005; Federmeier et al., 2010; Lau et al., 2013; Brothers et al., 2015, 2017).

When compared to young adult populations, healthy older adults have consistently shown reduced and delayed N400 effects of cloze probability (reviewed in Kutas and Iragui, 1998; Federmeier, 2007; Wlotko and Federmeier, 2012). An important debate in the field of language comprehension is whether these age-related changes can be primarily explained by reduced reliance on predictive mechanisms in older adults. The current study employs an active prediction paradigm (Brothers et al., 2015) to dissociate the neural effects of lexical prediction from other types of contextual support. In doing so, we are able to examine the locus of changes in contextual processing in older readers.

In young adults, Brothers et al. (2015) showed that the benefits of accurate predictions occurred very early during lexical processing and

* Correspondence to: Departments of Medical Social Sciences and Neuroscience (NUIN), Feinberg School of Medicine, Northwestern University, USA.
E-mail address: shruti.dave@northwestern.edu (S. Dave).

https://doi.org/10.1016/j.neuropsychologia.2018.05.023
Received 24 October 2017; Received in revised form 21 May 2018; Accepted 25 May 2018
Available online 28 May 2018

preceded the facilitative effects of other types of contextual support. The present study examines whether this pattern is preserved in older adult readers,who have been suggested to be less efficient at online processing due to general neural decline (e.g., Federmeier, 2007; Wingfield and Grossman, 2006; Wlotko et al., 2010), sensory deficits (e.g., Gordon et al., 2016; Rayner et al., 2010; Tun et al., 2009), or shifted strategies (e.g., Davis et al., 2008; Rayner et al., 2009; Stine-Morrow, 2007). We further address whether aging affects the allocation of neural resources to prediction during discourse processing, and what this may mean for understanding how older adults construct meaning while reading.

1.1. Electrophysiological correlates of prediction

In ERP research, predictive processing has been associated with modulations of the amplitude of the centro-parietal N400 effect (Kutas and Hillyard, 1984). A reduced N400 is found not only to critical words whose semantic features are predictable given prior discourse context (e.g., Boudewyn et al., 2015; reviewed in Swaab et al., 2012; Kuperberg et al., 2018; Kutas and Federmeier, 2011), but also to words whose agreement features are consistent with a predicted noun downstream (e.g., Szewczyk and Schriefers, 2013). While the N400 has been the primary ERP effect examined in studies of language comprehension, two other components – the N250 and post-N400 positivity – also show sensitivity to predictability manipulations.

Early facilitative effects of prediction on processing of visual word form are reflected in modulation of the N250 (Grainger and Holcomb, 2009; Lau et al., 2013; Brothers et al., 2015). In contrast to the N400, the N250 is typically maximal over more anterior electrode sites, suggesting that the N250 and the N400 are not generated by identical neuronal sources, and may reflect dissociable processing during reading comprehension. Grainger and Holcomb (2009) observed that the N250 was sensitive to orthographic level processing in repetition priming paradigms, finding a reduced N250 to repeated target words when participants were unaware of the identity of the prime (i.e., masked priming). The N250 has been more elusive when the prime is fully visible in word priming paradigms, as well as in studies manipulating predictability of words in sentence and discourse contexts – presumably because early anticipatory effects on word-form level processing are small relative to later effects on semantic processing (but see Lau et al., 2013; Brothers et al., 2015).

In addition to word processing benefits, ERP studies of prediction have also identified a later ERP, the anterior *post-N400 positivity* (PNP), which is sensitive to more prolonged, re-interpretive processes (500–1200 ms). PNP amplitudes are larger to unexpected critical words appearing in highly predictable contexts (Federmeier et al., 2007), suggesting that the PNP may reflect costs involved in detecting and resolving an incorrect prediction. More recently, larger PNPs have also been found for incorrectly predicted words in more moderate cloze contexts (e.g., Brothers et al., 2015), indicating that PNPs may additionally index updating of discourse representations in light of new, unanticipated information (Van Petten and Luka, 2012). Finally, Kuperberg et al. (2018) suggest that PNP effects may reflect adaptation processes occurring when predicted items are not presented, requiring an inference shift to an unexpected word.

1.2. Aging and predictability ERPs

In electrophysiological studies of healthy aging, effects of cloze probability on the N400 are both reduced in amplitude and delayed by approximately 30–50 ms in older relative to younger adults (e.g., Kutas and Iragui, 1998; Federmeier et al., 2002; Federmeier, 2007; Wlotko et al., 2010; Kutas and Federmeier, 2011; Wlotko et al., 2012). Age-related changes in the N400 effect have been suggested to reflect decreased ability to benefit from – and therefore reduced reliance on – prior contextual information (Federmeier et al., 2002; Wlotko and Federmeier, 2012), resulting in increased reliance on bottom-up sensory processing (e.g., DeLong et al., 2012; Lindenberger and Mayr, 2014).

However, studies of aging examining effects of cloze probability have rarely investigated effects preceding the N400 (but see Federmeier et al., 2010; DeLong et al., 2012), and effects following the N400 (e.g., PNPs) have not been consistently reported (e.g., Wlotko and Federmeier, 2012; Wlotko et al., 2012). Moreover, sensitivity to context may be heterogeneous in aging populations, as suggested by research examining inter-individual variability in the amplitude of ERP effects in older readers. In one set of studies, older adults with higher scores on a test of category verbal fluency (i.e., generating category exemplars) showed more young-like ERP effects (i.e., N400 or PNP amplitudes; Federmeier et al., 2010; DeLong et al., 2012), suggesting a critical role for semantic retrieval processes during lexican prediction. Neuroimaging and lesion studies have further revealed associations between category fluency and frontal cortical activation (Stuss et al., 1998; Gourovitch et al., 2000), leading some to hypothesize that preserved frontal lobe function may subserve frontally mediated generation of online lexical predictions - especially in aging populations (e.g., Federmeier et al., 2010).

1.3. The current study

In the present study, we use an active prediction paradigm (Brothers et al., 2015) to examine the neural effects of successful prediction on a trial-by-trial basis. In this paradigm, readers were presented with two-sentence passages, and were asked to try to predict the final word of each passage before it is presented. Each passage was constrained towards two equally likely final words (e.g., Table 1). In one condition, passage-final words were one of these two equally likely items (moderate cloze condition). In a second condition, the passage-final moderate cloze words were replaced by an unpredictable but plausible low cloze word (low cloze condition). At the end of each passage, readers were instructed to report whether they had accurately predicted the passage-final items, and this report was used to sort moderate cloze condition trials by prediction accuracy.

When examining ERP effects of prediction accuracy (i.e., between moderate cloze words that were accurately or inaccurately predicted), young adults showed reduced N250 and N400 amplitudes for correctly predicted words. These effects significantly preceded N400 effects of contextual support (i.e., between moderate and low cloze words that were inaccurately predicted) by approx. 100 ms. Additionally, graded effects of contextual support and prediction accuracy emerged on the anterior PNP; while low cloze items elicited the largest frontal positivities, inaccurately predicted moderate cloze words generated a larger late positivity than accurately predicted passage completions.

In the current study, by separating the effects of prediction accuracy and contextual support with this paradigm, we aimed to test whether older adults show *specific* deficits in predictive processing. According to prediction-deficit accounts of aging, older adults should self-report fewer successful predictions than younger adults in moderately constraining sentence contexts. These accounts would also predict that older adults should show larger reductions in prediction-related ERP effects relative to ERP effects related to contextual fit. Finally, older adults with young-like verbal fluency abilities should show preserved prediction effects on both early and late ERP components, relative to older adults with impaired production systems. If this is not the case, we must re-evaluate how predictive mechanisms are engaged by older populations.

2. Materials and methods

2.1. Participants

Young adult participants included 24 undergraduates at the

Table 1
Sample stimuli. Passages in moderate and low cloze conditions were equated for contextual constraint, but in the low cloze conditions, a moderate cloze final word was replaced by a low cloze word. As can be seen in Table 1, the passage final word was identical in both supportive and unsupportive passages.

Passage Type	*Moderate Cloze Final Word (40-60%) Condition*		*Low Cloze Final Word (0-7%) Condition*
Discourse Context: *Sentence 1*	Debbie wanted a long crunchy vegetable to dip into the ranch dressing.		At the checkout, Debbie needed a treat that would quiet her fussy children.
Discourse Context: *Sentence 2*	She decided to buy some…		She decided to buy some…
Participant's Expected Word	**Celery**	**Carrots**	**Candy, Cookies**
Actual, Presented Word	**…Celery**	**…Celery**	**…Celery**
Summary: *contextual support and accuracy of prediction*	*contextual fit, accurate prediction*	*contextual fit, inaccurate prediction*	*lack of contextual support, inaccurate prediction*

University of California, Davis (13 females; mean age: 20.5; range: 18–33). 24 older adult participants (14 females; mean age: 71.98 years; range 64–79) were recruited via flyers and newspaper advertisement from the greater Davis area in Yolo County, California. All young and old adults were native, monolingual speakers of English, with normal or corrected-to-normal vision and no known history of psychiatric or neurological disorders. Participants who reported major head trauma or who were taking neuro-active prescription medication in the preceding six months were excluded. Both groups of participants were right-handed, per self-report and the Edinburgh Handedness Inventory (Oldfield, 1971). All older adults reported completing high school, and all but one participant additionally completed post-secondary schooling (years of post-secondary education: $M = 4.88$, $SD = 2.53$). Older adults thus generally reported more education than undergraduates, but both groups came from similar educational backgrounds.

Young adults were compensated for participation with course credit; older adults received $10 per hour. Both groups participated after providing written informed consent to a protocol approved by the Institutional Review Board at the University of California, Davis. Data from two additional participants in each age group were excluded from the analyses due to excessive artifacts in EEG recordings.

Both groups additionally performed two verbal fluency tests (Controlled Oral Word Association Test; Benton, 1968). Participants were asked to produce as many words as possible that (i) began with a particular letter (F, A, S) and (ii) belonged to a semantic category (fruits, animals, non-fruit items in a supermarket); one minute was allotted for each letter or category. Correct responses to the three letters were summed to calculate a *letter verbal fluency score*, while correct responses to the three semantic categories were summed to calculate a *category verbal fluency score.* Previous research correlating verbal fluency scores with ERP amplitudes in aging has alternately used category fluency (e.g., Federmeier et al., 2010) or both category and letter fluency (e.g., Delong et al., 2010). Here we test letter and category fluency separately.

Older adults scored higher than young adults on category fluency (old: $M = 50.94$, $SD = 10.58$; young: $M = 44.71$, $SD = 10.82$; $t(44) = 3.18$, $p = .003$), with scores generally comparable to educated older adults in similar studies (e.g., Federmeier et al., 2002). Young adults performed slightly better than older adults on the letter fluency task, but the difference was not significant (old: $M = 54.92$, $SD = 9.88$; young: $M = 57.80$, $SD = 11.20$; $t(44) = 1.30$, $p = .20$).

2.2. Stimuli

The stimuli were identical to those reported in Brothers et al. (2015). 360 two-sentence passages were generated with 180 unique sentence-final critical words (e.g., Table 1). All passages were constrained towards two equally likely words. For two thirds of the passages, one of the moderate cloze words was presented as the passage final word (moderate cloze condition: 50.7%; range: 40 – 60%). For the remaining third of passages, the final critical word was replaced with a highly unexpected, though plausible, word (low cloze condition: 0.9%; range: 0 – 7%). Importantly, the same passage final words were used in both moderate and low cloze conditions.

Cloze norms obtained from 160 young adults (undergraduates, Brothers et al., 2015) showed that low and moderate cloze passages differed significantly in cloze probability of the passage final word ($p < .001$), but did not differ in constraint (51.1% for moderate cloze; 51.8% for low cloze passages). Similar results emerged for cloze norms collected from 120 older adults (mean age: 63.3; range: 55–78) via Amazon Mechanical Turk. For moderate cloze passages, final words produced an average cloze of 50.2% (range 30–70%) in older adults (versus 50.7% in young adults); low cloze passage final words produced an average cloze of 1.1% (range 0–10%) in older adults (versus 0.9% in young adults)

Each participant read 120 moderate and 60 low cloze passages that were randomly intermixed, such that each context and critical word was presented once per participant. The passages were counterbalanced across three experimental lists so that each target word appeared equally often in moderate and low cloze passages.

2.3. Procedure

During EEG recording, participants were seated in an electrically-shielded, sound-attenuated booth while stimuli were presented on an LCD monitor (at a distance of 90 cm). Following a short practice session, passages were presented in six blocks, with short breaks between each. Participants were instructed to read each passage for comprehension, and to use the context of both sentences to predict the passage final word. Participants were told that there were no "correct" predictions, and that they should indicate via button press whether the word they had predicted matched the word that was actually presented. The response hand for the prediction accuracy decision was counterbalanced across participants.

The first sentence appeared on the monitor in full; participants were asked to press a button when they had read and understood the first sentence, following which a central fixation cross appeared for 1000 ms to orient the participant's eyes. The second sentence of the passage was then presented in the center of the screen at a Rapid Serial Visual Presentation (RSVP) rate of 300 ms per word with a stimulus onset asynchrony of 600 ms. After the final (target) word of a passage was presented, 1700 ms of blank screen was shown, followed by a question mark. When the question mark appeared, participants pressed to indicate whether they had accurately predicted the presented final word of the passage. After a response was recorded, the experiment automatically proceeded to the next trial after 1000 ms.

2.4. EEG recording

EEG was recorded from 29 tin electrodes, mounted in an elastic cap (ElectroCap International). Additional electrodes were placed below and on the outer canthi of the left and right eyes in order to monitor blinks and eye movements. All electrode impedances were kept below 5 kΩ. The EEG signal was amplified using a Synamps Model 8050 Amplifier with bandpass cutoffs at 0.05 and 30 Hz, and was digitized continuously at a sampling rate of 250 Hz (along with stimulus codes used for subsequent averaging). All channels were initially referenced to an electrode placed over the right mastoid and later re-referenced to the average of the right and left mastoids. Data processing and analysis was performed using SCAN (Compumedics Neuroscan) and Matlab (The MathWorks, Natick, MA), with the EEGLAB toolbox and ERPlab plugin (Luck, 2005).

Independent component analysis (ICA) was used to decompose EEG responses into additive subcomponents with fixed scalp distributions and independent time courses to isolate and remove eye blink components (Li et al., 2006). Single-trial waveforms were screened for amplifier blocking, muscle artifacts, and horizontal eye movements over epochs of 1500 ms, starting 300 ms before the onset of critical target items. Trials contaminated by artifacts were not included in the grand average. 7.2% of trials were excluded due to artifacts in young adults, and 8.3% were excluded in older adults (non-significant difference: $t(46) = 0.61$, $p = .54$). After artifact rejection, trials were sorted into three bins based on cloze probability and prediction accuracy. Average ERPs were then calculated for each bin, resulting in ERPs for (i) accurately predicted target words in moderate cloze passages (Moderate Cloze Predicted), (ii) inaccurately predicted target words in moderate cloze passages (Moderate Cloze Unpredicted), and (iii) inaccurately predicted target words in low cloze passages (Low Cloze Unpredicted). Fewer than 4% of final words to low cloze passages were selected as accurately predicted (see Behavioral Results); these trials were excluded from ERP analyses.

3. Results

3.1. Behavioral results

Young adults reported correctly predicting the final word for 48.9% of moderate cloze passages (range: 32–73%, $SD = 10.6\%$), and older adults for 51.8% (range: 25–77%, $SD = 19.6\%$), with no significant difference between age groups ($t(46) = 0.45$, $p = .65$). Older adults showed more within-group interindividual variability in self-reported accuracy than younger adults ($p < .01$), but all values were in the same range as the 50.7% reported for young adults by Brothers et al. (2015). As moderate cloze items were selected from a tight range of cloze probabilities (40–60% cloze), individual lexical items were approximately equally likely to appear as unpredicted or predicted targets across participants.

Young adult participants reported correctly predicting 3.2% of low cloze passage final words (range: 0–13%, $SD = 3.8\%$), and older adults 2.7% (range: 0–18%, $SD = 5.3\%$). Again, there was no difference in prediction accuracy between groups ($t(46) = 0.6$, $p = .54$), and no difference in interindividual variability across groups ($p > .4$). These values were similar to the cloze values (average: 0.9%) obtained in our off-line norming study. Older adults could thus reliably perform the task, and their self-reported accuracy did not differ from young adults' for either moderate or low cloze passages.

3.2. ERP mean analysis results

Grand average ERP waveforms for young and older readers are plotted for the three critical conditions (Moderate Cloze Predicted, Moderate Cloze Unpredicted, Low Cloze Unpredicted) in Fig. 1.

For all three conditions across both age groups, overlapping baseline activity was followed by visual P1, N1, and P2 components. In both groups, this was followed by negative deflections for both unpredicted conditions relative to predicted moderate cloze items. In young adults, this divergence between predicted and unpredicted conditions began approximately 200 ms after stimulus onset and peaked at approximately 400 ms. In older adults, this waveform appeared reduced and delayed (maximal around 450 ms). In young adults, waveforms for unpredicted moderate cloze and low cloze conditions began to diverge approximately 300 ms post-stimulus, with more negative waveforms for the low cloze condition. Older adults showed delayed and reduced waveforms in both conditions, but as was observed for young adults, the peak of moderate cloze condition waveforms preceded that of the low cloze condition. For both young and older adults, these negative waveforms were followed by a positive shift in the unpredicted moderate cloze and low cloze conditions (maximal over anterior electrode sites).

To analyze these differences statistically, we performed mixed-subjects repeated-measures analyses of variance (rANOVAs) for the 3-level within-subjects factor of Condition (Moderate Cloze Predicted, Moderate Cloze Unpredicted, Low Cloze Unpredicted) and 2-level between-subjects factor of Age (Young Adults, Older Adults). Any significant effects of Condition were followed up by pair-wise comparisons for effects of prediction accuracy (*Prediction* Conditions: Moderate Cloze Predicted, Moderate Cloze Unpredicted) and effects of context independent of prediction accuracy (*Context* Conditions: Moderate Cloze Unpredicted, Low Cloze Unpredicted), reported in Table 2.[1] Interactions with the between-group factor of Age were followed up with analyses for each age group separately (reported in Table 3).

To analyze topographic distribution of effects over the scalp, rANOVAs included a 2-level factor of Hemisphere (Left, Right) and a 3-level factor of Anteriority [Frontal (FP1/2, F7/8, F3/4), Central (FC5/6, FC1/2, C3/4, CP1/2, CP5/6), Posterior (T5/6, P3/4, O1/2) electrode sites]. We conducted rANOVAs on mean amplitudes measured in N250 (200–300 ms) and early N400 (300–400 ms) time windows. Because numerous studies have demonstrated age-related slowing of ERP effects (e.g., Federmeier and Kutas, 2005; Kutas and Iragui, 1998; Polich, 1996), we also performed similar rANOVAs in 50 ms delayed windows (e.g., 250–350 ms) in order to determine if ERP effects of Prediction and/or Context are significant in later windows for older adults. We further conducted a similar set of rANOVAs for effects observed in the late positive (PNP, 600–900 ms) window.

We refer to Table 2 (omnibus rANOVAs including Age) and Table 3 (rANOVAs conducted independently for young and older adults) for *F*, *p*, and *df* values for each comparison described below. Topographic plots of Prediction and Context effects are displayed for young and older adults in Fig. 2; separate plots were generated across incremental

[1] In our study, Accurate Prediction meant that subjects indicated that they had successfully predicted the sentence-final word as it appeared on the screen. Inaccurate Prediction meant that subjects indicated that their specific prediction was incorrect. We recognize that linguistic prediction is not limited to lexical form, and that participants likely made predictions at semantic and event levels as well, but chose these labels because they match the definitions in the task instructions.

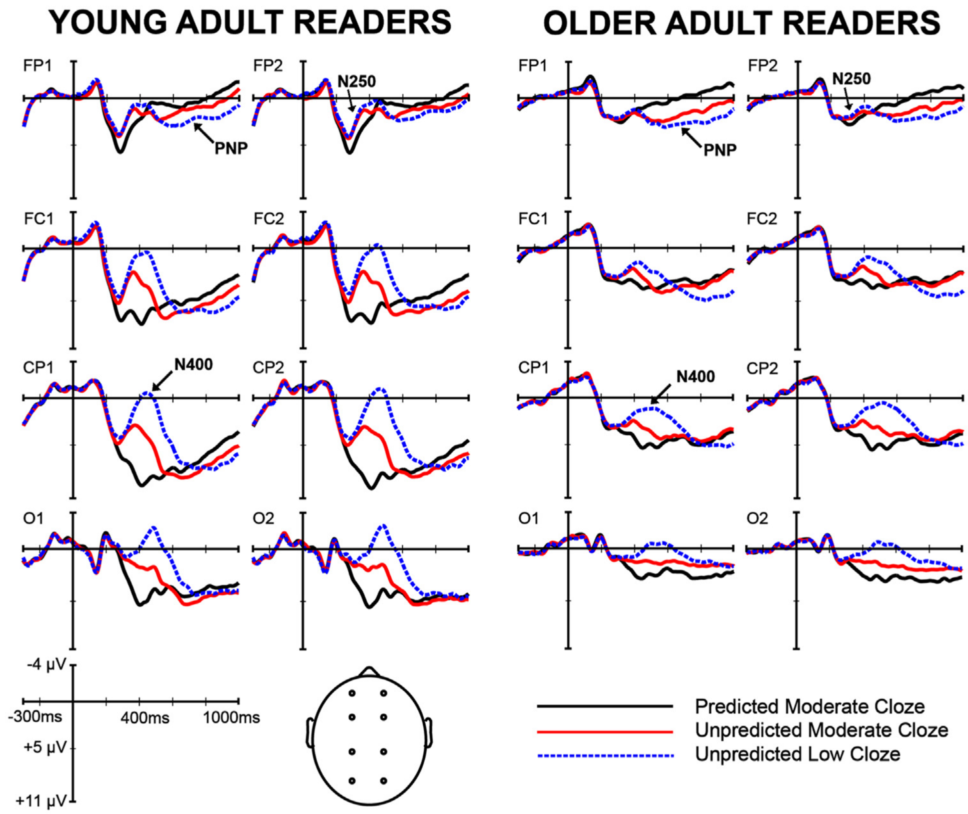

Fig. 1. Averaged event-related potentials for passage-final critical words for young (left) and older adult (right) readers. Averages are shown for unpredicted low cloze final words, unpredicted moderate cloze final words, and predicted moderate cloze final words.

100 ms windows in order to visualize when effects became significant, as well as the distribution of those significant effects over the scalp.

3.2.1. N250 Epoch

3.2.1.1. 200–300 ms. In the typical N250 window, young adults in the current study showed similar effects of Prediction to the young adults studied by Brothers et al. (2015). As seen in Fig. 2 (top left), this fronto-centrally distributed negativity was reduced for accurately predicted relative to unpredicted moderate cloze words. In contrast, no significant effects of prediction accuracy were found in this epoch for older adults. Thus, in the 200–300 ms epoch, young – but not older – adults showed facilitation when processing words whose identity was accurately predicted. As in Brothers et al., no effects of Context emerged for either age group in this window, suggesting that Prediction benefits readers prior to effects of Context.

3.2.1.2. 250–350 ms. In contrast to the previous window, older adults showed significant Prediction effects in this delayed epoch, though these effects were quantitatively smaller than those found in young adults. Topographic plots of Prediction in older adults resembled those of young adults in the earlier 200–300 ms epoch, i.e., maximal over fronto-central sites, suggested the N250 was temporally delayed but showed a typical spatial distribution in older readers.

Interestingly, N250 effects of Prediction were somewhat more right lateralized in older compared to younger readers. One explanation for this distributional difference may be that older adults recruit additional neural resources from the right hemisphere during lexical prediction (e.g., through over-activation via compensation-related utilization of neural circuits (CRUNCH); Reuter-Lorenz and Cappell, 2008).

3.2.2. Early N400 Epoch

3.2.2.1. 300–400 ms. Prediction significantly influenced ERP waveforms for both age groups in the 300–400 ms window. The distribution of Prediction effects changed from earlier time windows, becoming more centralized (Fig. 2) and typical of N400 effects (Kutas and Federmeier, 2011). Thus Prediction influences both N250 and later N400 components in both young and older readers.

Main effects of Context were found in the 300–400 ms window in young adults, as young readers showed larger negativities for unpredicted, contextually incongruent (i.e., low cloze) items relative to unpredicted moderate cloze items. Like effects of Prediction in this window, Context effects were centrally maximal. In contrast, main effects of Context did not emerge in this window in older adults.

3.2.2.2. 350–450 ms. In a 50 ms delayed window, effects of Context were found for both age groups; nonetheless, these effects were again larger for younger adults than for older adults. This finding suggests that older adults do show an N400 effect of Context, but this effect is delayed relative to younger readers (as in Federmeier and Kutas, 2015). In young adults, Context effects in this window were central-posterior, i.e., typically distributed for an N400 effect. Older adults showed a similar centro-posterior distribution, but the effect was more right-lateralized than in young adults (as with Prediction effects discussed above).

3.2.3. PNP Epoch

As seen in Fig. 1, PNP effects for both Prediction and Context were found in young and older adults; unlike N250 and N400 effects, no significantly differences in PNP amplitude emerged as a function of age. Readers in both age groups had larger positivities for unpredicted moderate cloze words relative to their predicted counterparts, and further showed even larger positive deflections for unpredicted and contextually incongruent low cloze items.

PNP effects of Prediction were frontally distributed in both age groups (Fig. 3). As in Brothers et al. (2015), young adults showed a left-lateralized frontal distribution of PNP effects of Prediction; in contrast,

Table 2
Omnibus rANOVAs separated for effects of Prediction (Condition: moderate cloze predicted, moderate cloze unpredicted) and Context (Condition: low cloze unpredicted, moderate cloze unpredicted). The rANOVAs for Prediction and Context include factors of Age (Young Adults, Older Adults), Condition (C: 2 levels), Anteriority (A: 5 levels), and Hemisphere (H: 2 levels). Findings are reported for the typical epochs (bolded): N250 (200–300 ms), early N400 (300–400 ms), and PNP (600–900 ms) and two additional 50 ms delayed epochs. Indicated in gray are Omnibus rANOVAs where no significant Condition by Age interaction was found. [Degrees of freedom: Age, Condition, Age x C, Age x C x H: *F*(1,46); Age x C x A, Age x C x A x H: *F*(4, 184)].

Epoch	Factor	Prediction		Context	
		F	p	F	p
200-300ms	Age	6.54	*	4.53	*
	Condition (C)	112.18	***	1.23	ns
	Age x C	2.99	ns	1.49	ns
	Age x C x A	9.28	**	1.59	ns
	Age x C x H	0.001	ns	4.47	ns
	Age x C x A x H	9.67	***	0.41	ns
250-350ms	Age	5.94	*	4.48	*
	Condition	66.65	***	1.51	ns
	Age x C	5.14	*	0.24	ns
	Age x C x A	8.95	**	2.39	ns
	Age x C x H	0.002	ns	3.69	ns
	Age x C x A x H	7.02	**	0.37	ns
300-400ms	Age	0.33	ns	0.003	ns
	Condition	20.50	***	9.90	**
	Age x C	1.08	ns	2.32	ns
	Age x C x A	3.13	*	2.14	ns
	Age x C x H	0.05	ns	10.43	**
	Age x C x A x H	0.07	ns	1.31	ns
350-450ms	Age	0.28	ns	0.58	ns
	Condition	21.25	***	54.99	***
	Age x C	1.63	ns	12.46	***
	Age x C x A	2.40	ns	3.29	*
	Age x C x H	1.06	ns	0.36	ns
	Age x C x A x H	0.86	ns	4.69	*
600-900ms	Age	20.57	ns	17.69	***
	Condition	352.50	***	3.59	*
	Age x C	19.64	***	0.11	ns
	Age x C x A	6.32	**	1.35	ns
	Age x C x H	0.22	ns	19.10	***
	Age x C x A x H	12.84	ns	1.21	ns

(Sig. levels: *$p < .05$; **$p < .01$, ***$p < .001$.).

Prediction PNPs in older readers had both a more bilaterally distributed and also had a more focused frontal distribution. Aging thus likely influences spatial distribution of neural activation in this window, in line with compensatory models suggesting hemispheric asymmetry reduction in older adults (HAROLD; Cabeza, 2002) and a posterior-anterior shifting of activation in aging (PASA; Davis et al., 2008).[2]

In contrast, Context effects in both age groups had very similar topographies: maximal effects over anterior electrode sites, with slight left lateralization. As such, age-related shifts in PNP spatial distribution appear to be specific to the processes associated with reconciling unpredicted (but predictable) items with the ongoing discourse representation.

3.3. Latency analyses

The pattern of results described above suggests that successful lexical prediction influences discourse processing earlier than supportive context in both young *and* older readers, with evidence of temporal delay in older adults. Critically, age-related prediction deficit hypotheses posit *specific* slowing of benefits of accurate prediction, i.e., delays for ERP effects of successful prediction that do not *generalize* to effects of contextual support independent of predictive accuracy. To examine whether unique prediction-related latency differences emerge for older adults relative to younger readers, we generated difference waveforms for our two effects of interest (Prediction, Context; Fig. 4).

To conduct latency analyses, we calculated the timing of the largest negative peak for the N400 (centro-parietal CP1/2, P3/4, POz, Pz electrodes in the 150–650 ms epoch) and the largest positive peak for the PNP (frontal FP1/2, AFz, Fz, F3/4 electrodes in the 400–1200 ms epoch). We directly compared the latency of the effects of Prediction and Context in young and older adults by conducting a mixed-effects ANOVA with a between-subjects factor of Age (Young Adults, Older Adults) and a within-subjects factor of Type (Prediction, Context).

N400 effects of Prediction preceded those of Context (Type: $F(1, 46) = 106.32$, $p < .001$), and effects of both Prediction and Context were significantly delayed in older adults relative to younger readers (Age: $F(1, 46) = 6.91$, $p = .01$). Critically, we observed no interaction (Age x Type: $F(1, 46) = 0.01$, $p = .99$; M_{young}: 34 ms, SD_{young}: 43 ms; M_{old}: 35 ms, SD_{old}: 64 ms), with a delay of approx. 35 ms in older adults for *both* Prediction and Context effects.

For the late frontal PNP, Prediction effects were approximately 88 ms earlier than those of Context (Type: $F(1, 46) = 7.08$, $p = .01$; M_{young}: 90 ms, SD_{young}: 129 ms; M_{old}: 86 ms, SD_{old}: 143 ms) in both age

[2] PNP effects of Prediction and Context were also found in the 50 ms delayed (650–950 ms window) for the entire population, as well as in both age groups separately ($ps < 0.01$).

Table 3
rANOVAs for the effects of Prediction (Condition: moderate cloze predicted, moderate cloze unpredicted) and Context (Condition: low cloze unpredicted, moderate cloze unpredicted), separated for young and older adults. The rANOVAs for Prediction and Context included the factors Condition (C: 2 levels), Anteriority (A: 3 levels), and Hemisphere (H: 2 levels). Findings are reported for the typical epochs (bolded): N250 (200–300 ms), early N400 (300–400 ms), and PNP (600–900 ms) and two additional 50 ms-delayed epochs. Indicated in gray are rANOVAs for which no main effects of Condition were found.

Epoch	Factor	Young Adults				Older Adults			
		Prediction		Context		Prediction		Context	
		F	p	F	p	F	p	F	p
200-300ms	Condition	7.96	***	0.30	ns	0.33	ns	0.01	ns
	C x A	6.51	ns	1.70	ns	0.42	ns	0.13	ns
	C x H	2.40	**	0.12	ns	3.53	ns	1.10	ns
	C x A x H	3.86	*	0.22	ns	0.67	ns	2.66	ns
250-350ms	Condition	36.51	***	0.57	ns	3.36	*	0.33	ns
	C x A	1.44	ns	1.62	ns	0.30	ns	0.25	ns
	C x H	9.12	***	2.10	ns	10.03	***	0.03	ns
	C x A x H	8.68	***	0.17	ns	0.57	ns	1.81	ns
300-400ms	Condition	64.82	***	9.90	**	25.46	***	1.57	ns
	C x A	16.26	***	3.08	ns	2.52	ns	7.66	**
	C x H	17.50	**	2.32	ns	12.41	**	4.83	*
	C x A x H	9.13	***	0.21	ns	0.96	ns	0.62	ns
350-450ms	Condition	73.83	**	72.23	***	23.35	***	7.35	*
	C x A	53.96	***	13.56	***	9.10	**	1.40	ns
	C x H	5.06	**	0.03	ns	12.98	**	6.44	*
	C x A x H	12.87	***	0.23	ns	6.21	**	0.21	ns
600-900ms	Condition	242.49	***	2.31	ns	115.63	***	1.13	ns
	C x A	37.56	***	2.39	ns	28.54	***	4.45	*
	C x H	0.58	ns	1.56	ns	3.81	ns	0.09	ns
	C x A x H	34.14	***	25.86	***	14.10	***	16.79	***

[Degrees of freedom: Condition, C x H: $F(1,23)$; C x A, C x A x H: $F(2, 46)$.].
(Sig. levels: * $p < .05$; ** $p < .01$, *** $p < .001$.).

groups. Here we observed no main effect of Age (Age: $F(1, 46) = 3.53$, $p = .07$), and no significant interaction ($F(1, 46) = 0.19$, $p = .66$).

Critically, the latency difference between the effects of Prediction and Context did not change as a function of age, indicating preserved primacy of prediction in aging.

3.4. Maximal amplitude analyses

The latency analyses reported above suggest that age-related *delays* in the N400 are unlikely to be related to specific impairment of predictive processing per se. Previous research (e.g., Federmeier and Kutas, 2005; Wlotko et al., 2012) and the current results (Mean Amplitude analyses) have found that older adults not only have later, but also smaller ERP effects of discourse context. Therefore, we also examined if age-related *reductions* in ERP amplitudes vary as a function of effect type (i.e., Prediction or Context). Brothers et al. (2015) calculated mean amplitude within 100 ms windows centered on the peak of each difference wave in young adults, finding similar amplitudes for Context and Prediction N400 effects. We performed similar analyses for N400 effects of Prediction (young adults: 355–455 ms, older adults: 390–490 ms) and Context (young adults: 458–558 ms, older adults: 494–594 ms), as well as PNP effects of Prediction (young adults: 709–809 ms, older adults: 758–858 ms) and Context (young adults: 799–899 ms, older adults: 844–944 ms). Age by Type rANOVAs were performed over the same frontal and centro-parietal clusters where effects were maximal (Fig. 5).

Consistent with our ERP mean amplitude analyses, Age reduced N400 amplitudes ($p < .001$) but had no effect on the size of the PNP ($p > .05$). Moreover this was the case for both Context and Prediction effects. Importantly, similar to our latency analysis, our mean-amplitude analysis show no interaction between Age and Type ($ps > 0.15$). For N400 effects, this finding indicates that age-related reductions are virtually identical for Prediction and Context effects, indicating that Prediction and Context contribute equally to N400 effects in young adults as in older adults. For PNP effects, this result demonstrates that effects of Prediction and Context on this component were similar across young and older adults.

Taken together, these latency and amplitude analyses suggest that aging does not disproportionately impair the ability to either generate lexical predictions (N400) or reconcile unpredicted but plausible information with the discourse representation (PNP). Before turning to a general discussion of our findings, we test one additional hypothesis related to predictive processing in aging (e.g., Federmeier et al., 2010), which suggests that predictive mechanisms in older adults may be related to production abilities, as quantified by our offline measures of verbal fluency (i.e., category and letter fluency scores).

3.5. Verbal fluency effects on ERP correlates of prediction and context

Regression analyses were generated to assess how performance on verbal fluency tasks may influence ERP effects. In these models, dependent variables included amplitudes of Prediction and Context effects on the N400 and PNP at 100 ms maximal windows (as in Section 3.3). Predictor variables included letter and category verbal fluency scores, as well as Age.

Significant models were generated for both N400 effects (Prediction N400: $R^2 = 0.406, p < 0.001$; Context N400: $R^2 = 0.346, p < 0.001$). Age significantly predicted the amplitude of both Prediction ($b = 0.59$, $t = 4.64$, $p < 0.001$) and Context ($b = 0.63$, $t = 4.75$, $p < 0.001$) N400 effects. However, neither letter nor context verbal fluency was

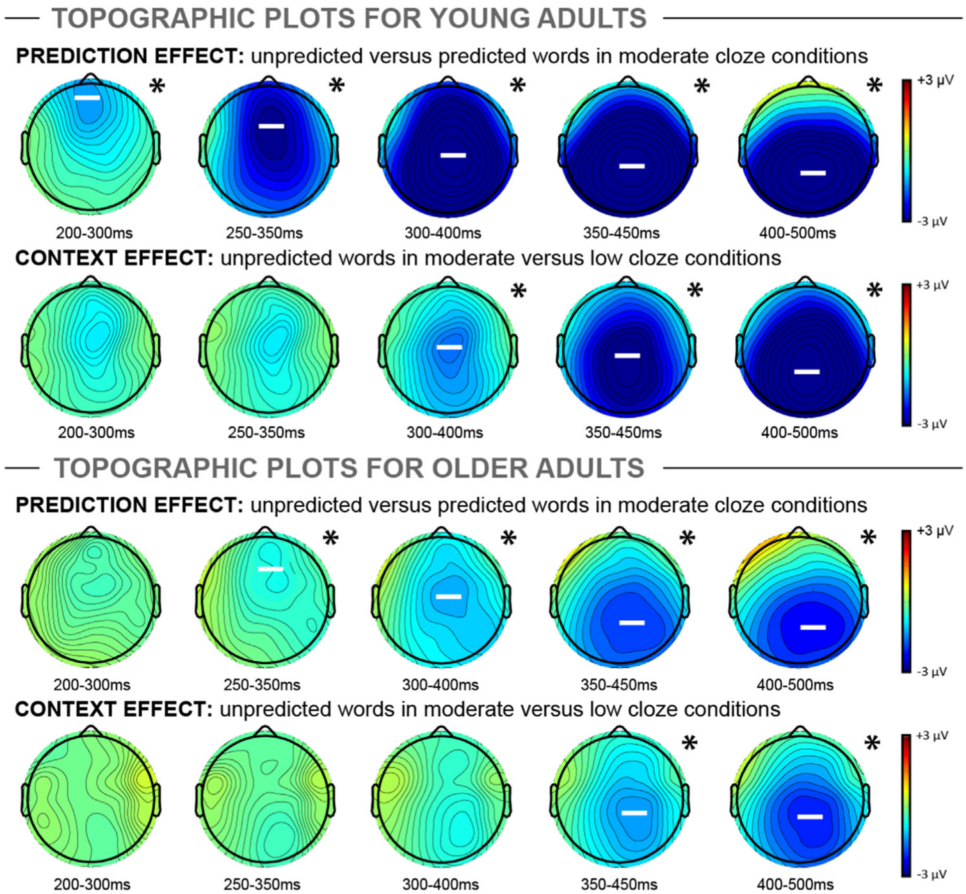

Fig. 2. Topographic distribution of N250 and N400 effects of Prediction and Context for young and older adults in five 100 ms epochs, each overlapping by 50 ms. White minus signs indicate where negative polarity effects are maximal. Asterisks mark epochs for which significant effects of prediction or context emerged.

found to predict either N400 effects of Prediction (*ps* > 0.20) or Context (*ps* > 0.15).

A non-significant model emerged for the PNP effect of Prediction (R^2 = 0.022, *p* = 0.80). In this model, neither Age nor verbal fluency measures were predictive of PNP amplitude (*ps* > 0.40). In a model generated for the PNP effect of Context (R^2 = 0.106, *p* = 0.17), age and letter verbal fluency were not predictive of Context PNP amplitude (*ps* > 0.55), while category verbal fluency did predict the amplitude of the Context PNP (*b* = 0.35, *t* = 2.24, *p* = 0.02). We addressed this finding in separate models for young and older adult readers, where both verbal fluency factors were included as predictors of PNP amplitude. In young adults, a non-significant model (R^2 = 0.041, *p* = 0.84) showed that the PNP effect of Context was not correlated with either verbal fluency measure (*ps* > 0.40). However, a significant model (R^2 = 0.38, *p* = 0.007) showed category verbal fluency (*b* = 0.59, *t* = 3.32, *p* = 0.003) contributed to the size of the PNP effect of Context in older readers (the effects of letter verbal fluency were not significant, *b* = 0.07, *t* = 0.38, *p* = 0.70).

To illustrate these results in older adults, we plotted ERP waveforms and topographic maps according to a median split of high and low verbal fluency (Fig. 6). Older adults with higher category verbal fluency showed larger PNP effects of contextual support in comparison to low category verbal fluency older adults, but verbal fluency did not modulate the amplitude of Prediction PNPs. Further, topographic plots of

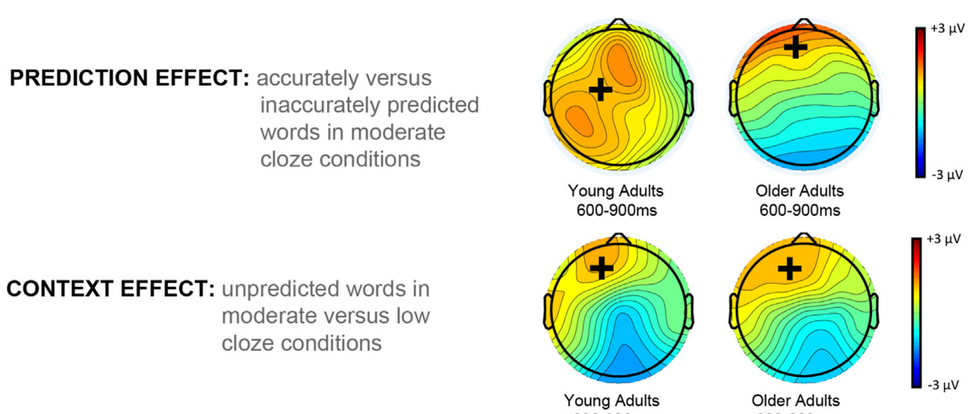

Fig. 3. Topographic distribution of significant PNP effects of Prediction and Context for young and older adult readers. Black addition signs indicate where positive polarity effects were maximal in the 600–900 ms window.

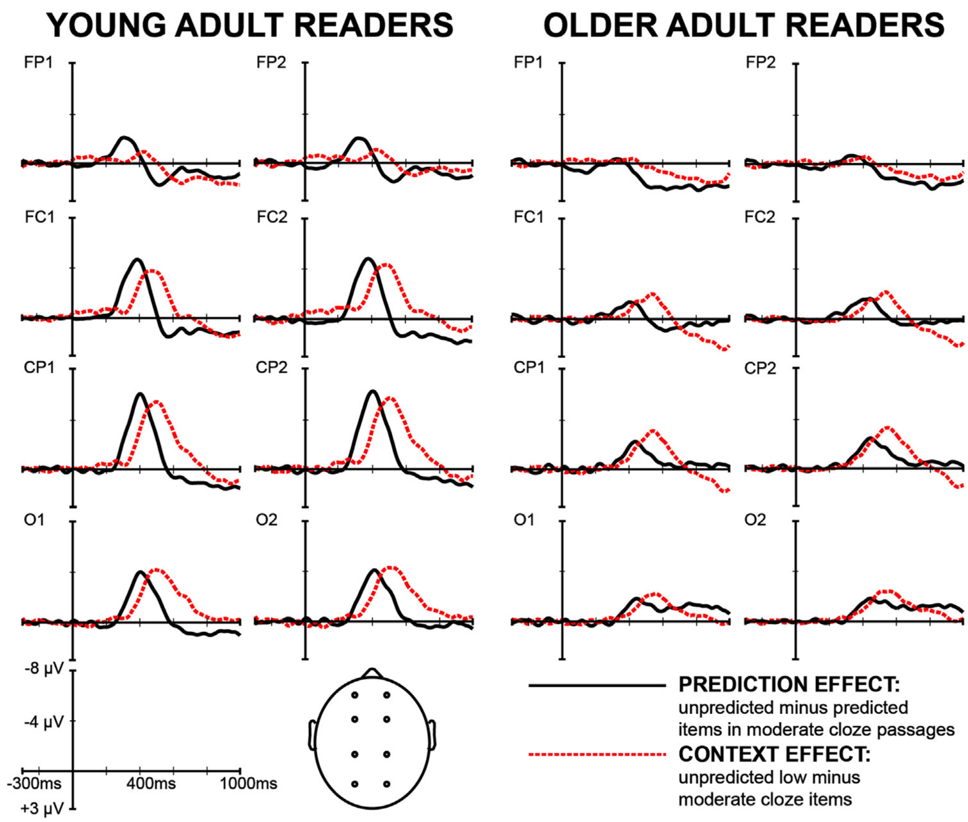

Fig. 4. ERP difference waves representing the effects of Prediction and Context for young adult (left) and older adult (right) readers.

the Context effect demonstrated stronger, more left-lateralized frontal effects emerging in older adults who performed better on tests of category fluency.

4. General discussion

Electrophysiological evidence supports the idea that younger readers employ predictive processing mechanisms during language comprehension in order to facilitate processing of upcoming words. However, studies in older populations have found reduced and delayed N400 facilitation following predictable contexts. This result has been taken to indicate that predictive processes are impaired in aging, and therefore comprehension in older readers may be less reliant on anticipatory mechanisms.

The current study tested this hypothesis by dissociating electrophysiological effects of lexical prediction from prediction-independent contextual facilitation. We found no age differences in the proportion of accurately predicted passage-final words, demonstrating that older adults are able to comprehend passages and predict upcoming words on par with young adults. ERP analyses revealed latency delays across the board in older readers, but critically, older adults showed clear neural benefits of prediction accuracy that preceded the effects of contextual support by approximately 100 ms, similar to younger readers. This suggests that the slowing of ERP responses in older adults is independent of prediction-specific mechanisms.

The overall magnitude of neural facilitation on the N250 and N400 components was reduced in older readers, but this reduction was not specific to effects of prediction accuracy; similar age-related changes emerged for N400 amplitudes of contextual facilitation. In contrast to prediction-deficit theories, older and younger adults in the present study showed similar relative contributions of prediction-based and prediction-independent mechanisms during reading comprehension. In addition, while we observed clear age-related reductions in the N400, no similar decline was observed in the amplitude of the late post-N400 positivity (PNP), either when simply processing unpredicted material, or integrating unpredicted information with the preceding discourse (see also Federmeier and Kutas, 2005; Wlotko et al., 2012). This result suggests that older adults may be shifting neural resources from processes related to facilitation (i.e., N400s) to processing reflecting discourse representation updating (i.e., PNPs). Implications of these results – as well as regression analyses addressing inter-individual variability in aging – are discussed below.

4.1. Age-related slowing of ERPs

As in prior studies of word-pair and discourse contexts (e.g., Federmeier and Kutas, 2005; Kutas and Iragui, 1998; Wlotko et al., 2012), N400 effects were delayed in older adults. To our knowledge, age-related temporal slowing of the N250 has not previously been investigated; our findings indicate similar slowing across these ERP components on the order of 35–55 ms. These results are consistent with the observation that older adults are slower readers overall, showing longer fixations and more frequent regressions during natural reading (reviewed in Gordon et al., 2016; Kliegl et al., 2004; Rayner et al., 2006; Choi et al., 2017).

Several factors may be involved in explaining delayed ERP effects in older adults. Temporal slowing may reflect reduced benefits of contextual constraint for older adults processing incoming words (Federmeier et al., 2010). In the present study, similar latency delays were observed in both N400 and N250 effects, suggesting that these processing delays may have originated at an earlier stage of lexical or sensory processing, which then produced down-stream consequences for both of these effects. We suggest that delayed lexical access in older adults may explain this pattern of generalized temporal slowing, although findings from the prior literature are somewhat equivocal on this point (Balota and Duchek, 1988; Bowles and Poon, 1985; Federmeier et al., 2007; Stern et al., 1991). An alternate, non-linguistic explanation may be a generalized age-related decline in processing

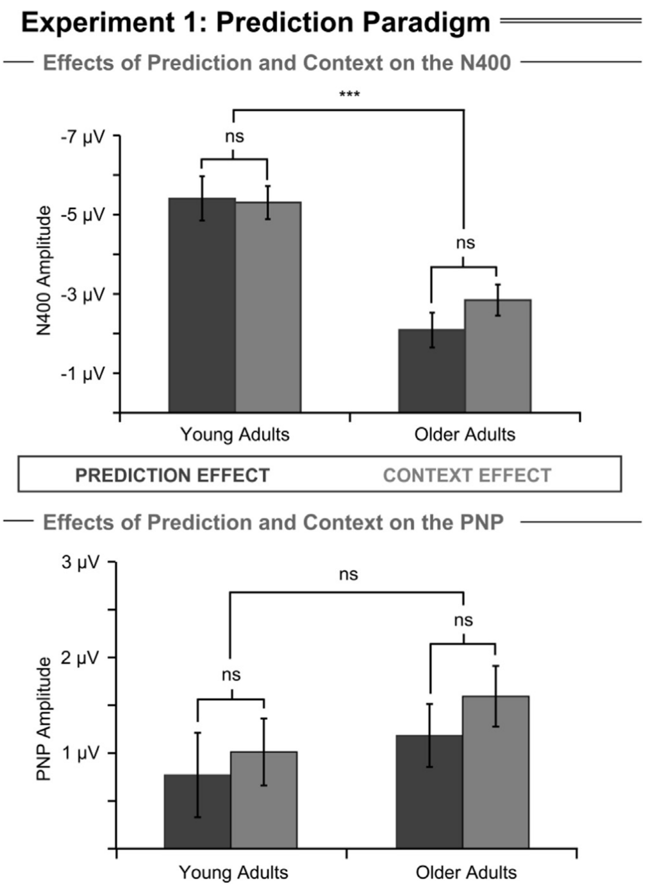

Fig. 5. Comparison of ERP amplitudes for Prediction and Context effects, presented for older and younger adults. Non-significant differences as a function of effect Type (Prediction, Context) are signified by ns.

speed caused by inefficient synaptic transmission (reviewed in Li et al., 2001), indexed as slowed effects across the ERP waveform. Within the current dataset, we observed small (10 ms) but significant (p (46) = 0.02) age-related slowing of an early visual component, the P1, suggesting that sensory slowing occurs alongside age-related delays in later language-related ERP components. In regression analyses with Age and P1 latency as separate predictors, P1 latency did not correlate to latency of the Prediction N400 (p = .10), though it significantly correlated with peak latency of the Context effect (p = 0.02). Age (ps > 0.05), however, predicted peak latency of both N400s effects of Prediction and Context. These results suggest that sensory slowing may provide only a partial explanation for age-related delays of the N400.

Delayed neural activity in aging is not specific to language-related paradigms. In stimulus categorization and oddball paradigms, the P3b component shows a linearized pattern of slowing with age (reviewed in Polich, 1996; Mueller et al., 2008) similar to the N400 (Kutas and Iragui, 1998). The P3b is believed to be associated with contextual updating and has been linked to attentional resource allocation and working memory. Further research should address common and potentially underlying factors, such as working memory capacity and attentional processing, which may slow context-dependent ERP components.

4.2. Facilitation for lexical predictions in aging

An important goal of this study was to address the source of older adults' attenuated N400 effects following predictability manipulations (reviewed in Federmeier, 2007). The prediction decision task employed in the current paradigm allowed us to gauge whether N400 reductions were tied to deficient neural mechanisms related to (i) generation and maintenance of predictions or (ii) other forms of contextual priming related to semantic association or differences in integration difficulty. Older adults showed qualitatively similar effects of prediction accuracy relative to younger adults, including a frontally distributed N250 effect that was delayed by approximately 50 ms. In combination with our behavioral results, this suggests that older adults are able to generate strong lexical predictions from context, and these predictions can facilitate early stages of word identification at the form level. This finding is consistent with recent eye-tracking results from Choi et al. (2017). In this study, the authors observed robust effects of cloze probability in both older and younger readers, with no differences in predictive processing between age groups (see also Huettig and Janse, 2016 for similar evidence from a visual world paradigm).

One possibility worth considering is that the current experimental task may have influenced the strength of predictive processing for both younger and older adults (see Brothers et al., 2015 for a discussion). Critically, however, the magnitude of age-related declines in the present experiment is notably similar to results found in previous studies employing simpler comprehension or memory tasks (e.g., Federmeier and Kutas, 2005). One

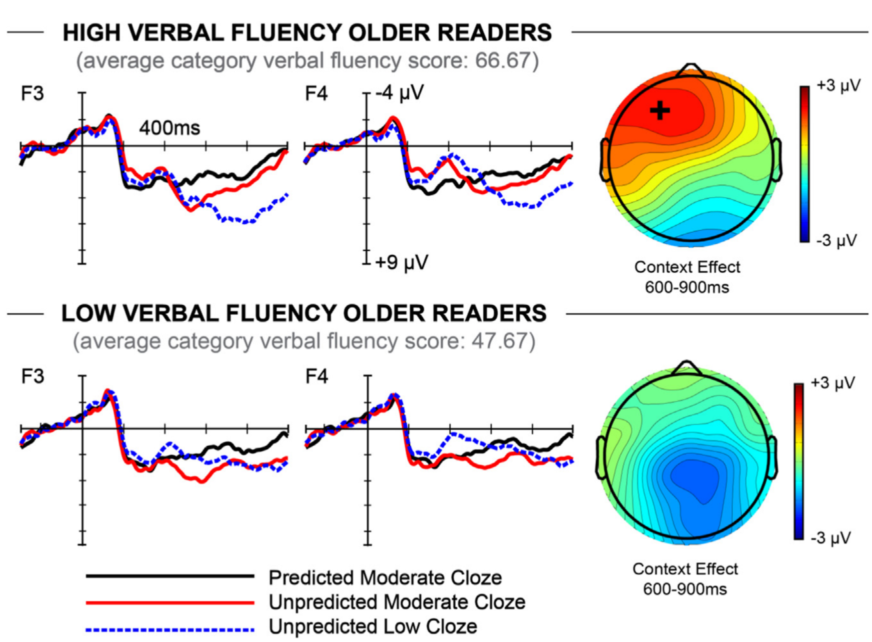

Fig. 6. Averaged event-related potentials at left and right lateral prefrontal electrodes, for older adults with high and low category verbal fluency (according to a median split). Topographic distributions of the PNP effects of Context (unpredicted low minus moderate cloze) are plotted for both high and low verbal fluency groups.

additional concern in the current task is whether the N250 reflects early form-level prediction (cf. Grainger and Holcomb, 2009; but see Ito et al., 2017), or if the N250 instead indexes prediction error or decision-related processes following an incorrectly predicted word (Nieuwenhuis et al., 2004). Importantly, because participants were asked to respond on *every* trial (and only after a delay), decision- or motor-related activity was not confounded with prediction accuracy. We further note that when the same experimental stimuli presented in the current study were presented without an overt prediction task, readers showed a highly similar pattern of ERP effects, including an early negativity between 200 and 300 ms over frontal electrode sites (Brothers et al., 2017). However, in line with strategy-based accounts of prediction (Kuperberg and Jaeger, 2016; Moors and De Houwer, 2006), both greater neural facilitation and larger predictive costs (i.e., N400s, PNPs) occurred for predictable items when readers were given an overt prediction task (as compared to task-free presentations of these stimuli). Thus while prediction is an everyday part of language comprehension, task goals can and do modulate predictive strategies (Lau et al., 2013; Brothers et al., 2017). It is currently an open question as to whether older adults similarly strategically alter predictive processing in response to task goals, and future research should assess the degree to which anticipatory modulation varies by age.

Age-attenuated N250 and N400 amplitudes may emerge from either language-specific or generalized sources. One plausible explanation for age-related changes observed in the current study is selectively impaired representations of context. Using tasks related to cognitive control (e.g., AX-CPT in Braver and Barch, 2002) and associative retrieval in free recall paradigms (e.g., Howard et al., 2006), researchers have determined that older adults, on average, show deficits in representing relevant contextual information. Such difficulties could underlie age-related differences in building discourse representations, which may impact both use of contextual information for prediction and integration mechanisms. Future research should investigate whether ability to represent context correlates with age-related reductions in electrophysiological signatures of both predictive processing and contextual facilitation.

Aging has also been associated with generalized differences in neural connectivity. ERPs reflect a summation of post-synaptic potentials generated by synchronous firing of pyramidal cells (Luck, 2005). Reduced arborization, synaptic transmission speed, or desynchronized activity in local and global networks (reviewed in Rommers and Federmeier, 2017) may explain latency as well as amplitude differences in aging (e.g., via attenuated summation of synchronous potentials). Current research suggests that declining neural efficiency might provide an underlying causal mechanism to explain slowed and reduced ERP effects during language processing (Dave et al., 2018). However, it is important to note that not all ERP effects were similarly attenuated in the current experiments; indeed, PNP effects were actually somewhat larger in older than younger adults. Thus, we suggest that neural decrements may not provide a direct or *complete* explanation of age-related changes in the current study, and that age-related differences in resource allocation may also play a critical role.

4.3. From N400s to PNPs

While age did not influence relative timing or amplitudes for effects of predictive accuracy and contextual support, PNP amplitudes were relatively larger than N400 effects for older as compared to younger readers. This suggests that older adults may have expended more neural resources on updating-related processes[3] (e.g., Van Petten and Luka, 2012; Thornhill and Van Petten, 2012; Brothers et al., 2015, 2017). This finding is critical to parsing possible age-related shifts in reading strategies, and shows commonalities with results found in self-paced reading, ERP, and structural and imaging literatures, as discussed below

In self-paced reading studies, aging impacts allocation of reading time to ends of sentences or discourses, i.e., wrap-up (e.g., Stine-Morrow et al., 2008; Stine-Morrow et al., 2006). Wrap-up time allows readers to update the ongoing contextual representation with their final sentential or discourse-level interpretation (i.e., much in the way that target items in the current study complete or "wrap-up" presented passages). Based on evidence that older adults consistently allocate more time to wrap-up (reviewed in Stine-Morrow and Payne, 2016), researchers have suggested that older readers are more likely to allocate resources strategically, such as by allotting more attention and time to conceptual integration (Stine-Morrow, 2007). Future studies should investigate within-subject correlations between reading time strategies and ERP effects gauging neural activation, in order to directly address potential theoretical links between older adults' wrap-up effects and post-N400 positivities.

To our knowledge, only three studies of language processing have identified ERP effects that do not show amplitude reductions in aging. In Federmeier and Kutas (2005), a manipulation of sentence constraint appeared to produce larger frontal PNPs in older readers than younger readers. Next, following grammatical number (syntactic) violations, Kemmer et al. (2004) saw similar-sized posterior P600 components in both age groups. Further, Wlotko and Federmeier (2012) (see Footnote 7) showed larger frontal negativities in the 600–900 ms window for older as compared to younger readers. Notably, these findings are all in late (600–900 ms) epochs for sentence-final words. This result may be explained by wrap-up allocation variability, as older adults may allot more resources across the board to representational updating.

Another important factor to consider is age-graded variability in the topographic distribution of electrophysiological effects. Older readers showed N250 and N400 effects of predictive accuracy, as well as N400 effects of contextual support that were largest over the right hemisphere. Further, younger readers in the current study showed significantly more left lateralized PNPs for predictive accuracy compared to older adults' frontally bilateral distributions. Models of neural activation (i.e, Cabeza et al., 2016; Davis et al., 2008; Reuter-Lorenz and Cappell, 2008) posit that age-related increases in the recruitment of right frontal areas might be related to compensation for reduced cognitive and neural resources in older adults. Importantly though, correlations between compensatory activation and task performance have been nebulous, to date (e.g., Düzel et al., 2011; Gutchess et al., 2006; Reuter-Lorenz and Cappell, 2008; Cabeza et al., 2002). Therefore we cannot draw performance-based conclusions regarding age-based differences in PNPs for prediction accuracy, and how they may compare to age-invariant PNP distributions for contextual support (Fig. 5). Future study should thus examine inter-individual factors (i.e., literacy, working memory) and task load effects on PNP topographies for inaccurately predicted items.

4.4. Verbal Fluency Influences on Late Positivities

In previous language ERP studies (i.e., Federmeier et al., 2007; Delong et al., 2014), late frontal positivities are elicited when contrasting the presentation of predicable words with plausible but unpredictable words in constraining contexts. This research, alongside regression analyses of contextual support (see Brothers et al., 2015), suggests that plausibility contributes critically to PNP amplitude, as opposed to lower-level semantic features (e.g., semantic overlap, lexical association). In the current study, manipulation of contextual support elicited a late frontal positivity ("Context" PNP) with a similar time course and topography as reported in previous research. Extant theoretical frameworks of the PNP (reviewed in Van Petten and Luka, 2012) have suggested that this component reflects resolution of unpredicted words with the ongoing discourse representation. Previous aging

[3] Wlotko and Federmeier (2012) have suggested that moderately constrained passages with one primary and few alternate completions are associated with a "frame-shifting" late frontal negativity generated when readers hold incorrect predictions for target words that are at 75–90% cloze probability. Further, Wlotko et al. (2012) suggest that older adults show increased frontal negativities relative to younger adults. As our stimuli fall outside this 75–90% cloze range (40–60% probability for moderate cloze passage completions), it is unlikely that our materials would elicit this "frame-shifting" late negativity.

literature has interpreted PNP amplitudes in older adults in light of these frameworks. The finding that this component's amplitude is modulated by verbal fluency (e.g., Federmeier et al., 2010; DeLong et al., 2012) has therefore been taken to suggest that verbal fluency influences older adults' resolution of unpredicted words.

However, in the current study, we further compared brain activity following unpredicted versus accurately predicted words of the same (moderate) cloze probability; this "Prediction" PNP shared time course and topography features with PNPs reported in the literature but was greater in amplitude relative to the Context PNP. Our results help to clarify previous verbal fluency-PNP findings in aging, demonstrating that high fluency older readers show larger late ERP effects when processing words that are contextually unpredictable (Context PNP) while fluency does not influence updating related to prediction accuracy (Prediction PNP). Therefore, the current paradigm suggests that verbal fluency effects in aging are *not* tied to prediction accuracy, but rather to contextual processing mechanisms.

One explanation for this finding may be that fluency scores correlate to the degree to which older adults engage in the "work" required to integrate plausible but unpredictable critical words. In line with this explanation, the same frontal cortical regions thought to subsume both production and predictive capacities (Federmeier et al., 2002, 2010) are also thought to maintain effortful processing in aging (e.g. Johnson et al., 2004; Reuter-Lorenz and Lustig, 2005). Effortful processes are more likely to be engaged when editing an ongoing discourse representation to incorporate low plausibility items, while unpredicted but semantically similar words are unlikely to challenge older adults' neural mechanisms to the same extent. As in Reuter-Lorenz (2002), we thus suggest that maintenance of frontal networks in older adulthood may aid in preserving higher-order effortful function, and verbal fluency may more generally act as a proxy measure for this neural reserve.

5. Conclusions

The findings of this study indicate that, relative to young adults, older adults have reduced and delayed facilitative effects of prediction accuracy and contextual support during discourse processing. However, we found no evidence that older adults show targeted deficits in lexical prediction. Instead, both younger and older adults were equally able to predict the final word of moderately constraining discourse contexts, and older adults showed qualitatively similar patterns of neural facilitation following correct predictions. Further, the costs of integrating inaccurately predicted or contextually incongruent words was roughly equivalent in older and young adult readers, although this late PNP effect had a more bilateral and fronto-polar distribution in older adults, and further correlated with verbal fluency in this population. In conclusion, prediction-deficit hypotheses cannot provide a compelling account of age-related differences in the use of context use across the lifespan, and alternative frameworks – including neural efficiency and resource allocation models – should be considered and tested in future studies.

Acknowledgements

This research was supported in part by NIA Grant 1R56AG053346-01A1. We would like to thank both anonymous reviewers and the section editor for their excellent comments on this manuscript.

References

Altmann, G., Mirković, J., 2009. Incrementality and prediction in human sentence processing. Cogn. Sci. 33 (4), 583–609.
Balota, D.A., Duchek, J.M., 1988. Age-related differences in lexical access, spreading activation, and simple pronunciation. Psychol. Aging 3 (1), 84–93.
Benton, A.L., 1968. Differential behavioral effects in frontal lobe disease. Neuropsychologia 6 (1), 53–60.
Braver, T.S., Barch, D.M., 2002. A theory of cognitive control, aging cognition, and neuromodulation. Neurosci. Biobehav. Rev. 26 (7), 809–817.
Brothers, T., Swaab, T.Y., Traxler, M.J., 2015. Effects of prediction and contextual support on lexical processing: prediction takes precedence. Cognition 136, 135–149.
Brothers, T., Swaab, T.Y., Traxler, M.J., 2017. Goals and strategies influence lexical prediction during sentence comprehension. J. Mem. Lang. 93, 203–216.
Boudewyn, M.A., Long, D.L., Swaab, T.Y., 2015. Graded expectations: predictive processing and the adjustment of expectations during spoken language comprehension. Cogn. Affect. Behav. Neurosci. 15 (3), 607–624.
Bowles, N.L., Poon, L.W., 1985. Aging and retrieval of words in semantic memory. J. Gerontol. 40 (1), 71–77.
Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging gracefully: compensatory brain activity in high-performing older adults. NeuroImage 17 (3), 1394–1402.
Cabeza, R., Nyberg, L., 2016. Cognitive Neuroscience of Aging: Linking Cognitive and Cerebral Aging. Oxford University Press.
Choi, W., Lowder, M.W., Ferreira, F., Swaab, T.Y., Henderson, J.M., 2017. Effects of word predictability and preview lexicality on eye movements during reading: a comparison between young and older adults. Psychol. Aging 32 (3), 232–242.
Clark, A., 2013. Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav. Brain Sci. 36 (3), 181–204.
Dave, S., Brothers, T.A., Swaab, T.Y., 2018. 1/f neural noise and electrophysiological indices of contextual prediction in aging. Brain Res. 1691, 34–43.
Davis, S.W., Dennis, N.A., Daselaar, S.M., Fleck, M.S., Cabeza, R., 2008. queue PASA? The posterior–anterior shift in aging. Cereb. Cortex 18 (5), 1201–1209.
DeLong, K.A., Groppe, D.M., Urbach, T.P., Kutas, M., 2012. Thinking ahead or not? Natural aging and anticipation during reading. Brain Lang. 121 (3), 226–239.
DeLong, K.A., Urbach, T.P., Kutas, M., 2005. Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. Nat. Neurosci. 8 (8), 1117–1121.
Düzel, E., Schütze, H., Yonelinas, A.P., Heinze, H.J., 2011. Functional phenotyping of successful aging in long-term memory: preserved performance in the absence of neural compensation. Hippocampus 21 (8), 803–814.
Federmeier, K.D., 2007. Thinking ahead: the role and roots of prediction in language comprehension. Psychophysiology 44 (4), 491–505.
Federmeier, K.D., Kutas, M., 2005. Aging in context: age-related changes in context use during language comprehension. Psychophysiology 42 (2), 133–141.
Federmeier, K.D., Kutas, M., Schul, R., 2010. Age-related and individual differences in the use of prediction during language comprehension. Brain Lang. 115 (3), 149–161.
Federmeier, K.D., McLennan, D.B., Ochoa, E., Kutas, M., 2002. The impact of semantic memory organization and sentence context information on spoken language processing by younger and older adults: an ERP study. Psychophysiology 39 (2), 133–146.
Federmeier, K.D., Wlotko, E.W., De Ochoa-Dewald, E., Kutas, M., 2007. Multiple effects of sentential constraint on word processing. Brain Res. 1146, 75–84.
Gordon, P.C., Lowder, M.W., Hoedemaker, R.S., 2016. Reading in normally aging adults. In: Cognitive-Linguistic Processes and Aging. Benjamins.
Gourovitch, M.L., Kirkby, B.S., Goldberg, T.E., Weinberger, D.R., Gold, J.M., Esposito, G., Van Horn, J.D., Berman, K.F., 2000. A comparison of rCBF patterns during letter and semantic fluency. Neuropsychology 14 (3), 353–360.
Grainger, J., Holcomb, P.J., 2009. Watching the word go by: on the time-course of component processes in visual word recognition. Lang. Linguist. Compass 3 (1), 128–156.
Gutchess, A.H., Welsh, R.C., Hedden, T., Bangert, A., Minear, M., Liu, L.L., Park, D.C., 2006. Aging and the neural correlates of successful picture encoding: frontal activations compensate for decreased medial-temporal activity. J. Cogn. Neurosci. 17 (1), 84–96.
Howard, M.W., Kahana, M.J., Wingfield, A., 2006. Aging and contextual binding: modeling recency and lag recency effects with the temporal context model. Psychon. Bull. Rev. 13 (3), 439–445.
Huettig, F., 2015. Four central questions about prediction in language processing. Brain Res. 1626, 118–135.
Huettig, F., Janse, E., 2016. Individual differences in working memory and processing speed predict anticipatory spoken language processing in the visual world. Lang., Cogn. Neurosci. 31 (1), 80–93.
Ito, A., Martin, A.E., Nieuwland, M., 2017. Why the A/AN prediction effect may be hard to replicate: A rebuttal to DeLong, Urbach & Kutas (2017). Retrieved from osf.io/preprints/psyarxiv/ayd3t.
Johnson, M.K., Mitchell, K.J., Raye, C.L., Greene, E.J., 2004. An age-related deficit in prefrontal cortical function associated with refreshing information. Psychol. Sci. 15 (2), 127–132.
Kliegl, R., Grabner, E., Rolfs, M., Engbert, R., 2004. Length, frequency, and predictability effects of words on eye movements in reading. Eur. J. Cogn. Psychol. 16, 262–284.
Kemmer, L., Coulson, S., De Ochoa, E., Kutas, M., 2004. Syntactic processing with aging: an event-related potential study. Psychophysiology 41 (3), 372–384.
Kuperberg, G.R., Jaeger, T.F., 2016. What do we mean by prediction in language comprehension? Lang., Cogn. Neurosci. 31 (1), 32–59.
Kuperberg, G.R., 2018. April). What event-related neural responses can tell us about language comprehension: A dynamic generative framework. Paper presented at In: Proceedings of the 31st Annual CUNY Sentence Processing Conference, Davis, CA.
Kutas, M., Federmeier, K.D., 2011. Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). Annu. Rev. Psychol. 62, 621–647.
Kutas, M., Hillyard, S.A., 1984. Brain potentials during reading reflect word expectancy and semantic association. Nature 307, 161–163.
Kutas, M., Iragui, V., 1998. The N400 in a semantic categorization task across 6 decades. Electroencephalogr. Clin. Neurophysiol./Evoked Potentials Sect. 108 (5), 456–471.

Lau, E.F., Holcomb, P.J., Kuperberg, G.R., 2013. Dissociating N400 effects of prediction from association in single-word contexts. J. Cogn. Neurosci. 25 (3), 484–502.
Li, S.C., Lindenberger, U., Sikström, S., 2001. Aging cognition: from neuromodulation to representation. Trends Cogn. Sci. 5 (11), 479–486.
Li, Y., Ma, Z., Lu, W., Li, Y., 2006. Automatic removal of the eye blink artifact from EEG using an ICA-based template matching approach. Physiol. Meas. 27 (4), 425–436.
Lindenberger, U., Mayr, U., 2014. Cognitive aging: is there a dark side to environmental support? Trends Cogn. Sci. 18 (1), 7–15.
Luck, S.J., 2005. Ten simple rules for designing ERP experiments. Event-related Potentials: A Methods Handbook. pp. 262083337.
Mueller, V., Brehmer, Y., Von Oertzen, T., Li, S.C., Lindenberger, U., 2008. Electrophysiological correlates of selective attention: a lifespan comparison. BMC Neurosci. 9 (1), 18.
Moors, A., De Houwer, J., 2006. Automaticity: a theoretical and conceptual analysis. Psychol. Bull. 132 (2), 297–326.
Nieuwenhuis, S., Holroyd, C.B., Mol, N., Coles, M.G., 2004. Reinforcement-related brain potentials from medial frontal cortex: origins and functional significance. Neurosci. Biobehav. Rev. 28, 441–448.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113.
Polich, J., 1996. Meta-analysis of P300 normative aging studies. Psychophysiology 33 (4), 334–353.
Rayner, K., Reichle, E.D., Stroud, M.J., Williams, C.C., Pollatsek, A., 2006. The effect of word frequency, word predictability, and font difficulty on the eye movements of young and older readers. Psychol. Aging 21 (3), 448–465.
Rayner, K., Castelhano, M.S., Yang, J., 2009. Eye movements and the perceptual span in older and younger readers. Psychol. Aging 24 (3), 755–760.
Rayner, K., Castelhano, M.S., Yang, J., 2010. Preview benefit during eye fixations in reading for older and younger readers. Psychol. Aging 25 (3), 714–718.
Rommers, J., Federmeier, K.D., 2017. Electrophysiological Methods. Research Methods in Psycholinguistics and the Neurobiology of Language: A Practical Guide.
Reuter-Lorenz, P.A., 2002. New visions of the aging mind and brain. Trends Cogn. Sci. 6 (9), 394–400.
Reuter-Lorenz, P.A., Cappell, K.A., 2008. Neurocognitive aging and the compensation hypothesis. Curr. Dir. Psychol. Sci. 17 (3), 177–182.
Reuter-Lorenz, P.A., Lustig, C., 2005. Brain aging: reorganizing discoveries about the aging mind. Curr. Opin. Neurobiol. 15 (2), 245–251.
Stern, C., Prather, P., Swinney, D., Zurif, E., 1991. The time course of automatic lexical access and aging. Brain Lang. 40 (3), 359–372.
Stine-Morrow, E.A., 2007. The Dumbledore hypothesis of cognitive aging. Curr. Dir. Psychol. Sci. 16 (6), 295–299.
Stine-Morrow, E.A., Miller, L.M.S., Hertzog, C., 2006. Aging and self-regulated language processing. Psychol. Bull. 132 (4), 582–606.
Stine-Morrow, E.A., Payne, B.R., 2016. Age differences in language segmentation. Exp. Aging Res. 42 (1), 83–96.
Stine-Morrow, E.A., Soederberg Miller, L.M., Gagne, D.D., Hertzog, C., 2008. Self-regulated reading in adulthood. Psychol. Aging 23 (1), 131–143.
Stuss, D.T., Alexander, M.P., Hamer, L., Palumbo, C., Dempster, R., Binns, M., Izukawa, D., 1998. The effects of focal anterior and posterior brain lesions on verbal fluency. J. Int. Neuropsychol. Soc. 4 (3), 265–278.
Swaab, T.Y., Ledoux, K., Camblin, C.C., Boudewyn, M.A., 2012. Language-related ERP components. Oxford Handbook of Event-related Potential Components. pp. 397–440.
Szewczyk, J.M., Schriefers, H., 2013. Prediction in language comprehension beyond specific words: an ERP study on sentence comprehension in Polish. J. Mem. Lang. 68 (4), 297–314.
Taylor, W.L., 1953. "Cloze procedure": a new tool for measuring readability. J. Bull. 30 (4), 415–433.
Thornhill, D.E., Van Petten, C., 2012. Lexical versus conceptual anticipation during sentence processing: frontal positivity and N400 ERP components. Int. J. Psychophysiol. 83 (3), 382–392.
Tun, P.A., McCoy, S., Wingfield, A., 2009. Aging, hearing acuity, and the attentional costs of effortful listening. Psychol. Aging 24 (3), 761–766.
Van Petten, C., Luka, B.J., 2012. Prediction during language comprehension: benefits, costs, and ERP components. Int. J. Psychophysiol. 83 (2), 176–190.
Wingfield, A., Grossman, M., 2006. Language and the aging brain: patterns of neural compensation revealed by functional brain imaging. J. Neurophysiol. 96 (6), 2830–2839.
Wlotko, E.W., Federmeier, K.D., 2012. Age-related changes in the impact of contextual strength on multiple aspects of sentence comprehension. Psychophysiology 49 (6), 770–785.
Wlotko, E.W., Federmeier, K.D., Kutas, M., 2012. To predict or not to predict: age-related differences in the use of sentential context. Psychol. Aging 27 (4), 975–988.
Wlotko, E.W., Lee, C.L., Federmeier, K.D., 2010. Language of the aging brain: Event-related potential studies of comprehension in older adults. Lang. Linguist. Compass 4 (8), 623–638.