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1/*f* Neural Noise and Electrophysiological Indices of Contextual Prediction in Aging

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Abstract

Prediction of upcoming words during reading has been suggested to enhance the efficiency of discourse processing. Emerging models have postulated that predictive mechanisms require synchronous firing of neural networks, but to date, this relationship has been investigated primarily through oscillatory activity in narrow frequency bands. A recently-developed measure proposed to reflect broadband neural activity – and thereby synchronous neuronal firing – is 1/*f* neural noise extracted from EEG spectral power. Previous research (Voytek et al., 2015) has indicated that this measure of 1/*f* neural noise changes across the lifespan, and these neural changes predict age-related behavioral impairments in visual working memory. Using a cross-sectional sample of young and older adults, we examined age-related changes in 1/*f* neural noise and whether this measure predicted ERP correlates of successful lexical prediction during discourse comprehension. 1/*f* neural noise across two different language tasks revealed high within-subject correlations, indicating that this measure can provide a reliable index of individualized patterns of neural activation. In addition to age, 1/*f* noise was a significant predictor of N400 effects of successful lexical prediction; however, noise did not mediate age-related declines in other ERP effects. We discuss broader implications of these findings for theories of predictive processing, as well as potential applications of 1/*f* noise across research populations.

1. Introduction

Studies of the effects of predictability during language comprehension in aging populations have traditionally examined cross-sectional differences that emerge when comparing groups of young versus older adult cohorts. Recent literature has sought to bolster this classic approach by considering the role of within-group variability. Across these studies, researchers have shown that neural indices of predictive processing vary between older adults as a function of their cognitive spans (e.g., Delong, Groppe, Urbach, & Kutas, 2012; Federmeier, Kutas & Schul, 2010; Federmeier, McLennan, Ochoa, & Kutas, 2002; Huettig & Janse, 2016). Considerably less research has examined how maintenance of neural function impacts prediction across the lifespan, though a number of researchers have proposed that strong, coherent neuronal networks likely underlie preservation of predictive

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processing in older adults (Federmeier et al., 2010; Peelle, Troiani, Wingfield, & Grossman, 2010; Wlotko, Federmeier, & Kutas, 2012). Testing this hypothesis directly requires finding a reliable measure of neuronal network dynamics that can be correlated with both age and predictive processing during language comprehension. One potential measure has recently been proposed by Voytek and colleagues (2015): $1/f$ neural noise extracted from spectral power in the EEG signal. Voytek et al. found that $1/f$ neural noise positively correlated with age, and these neural changes explained age-related decline in visual working memory performance. Here we investigate whether there are similar age-related differences in $1/f$ neural noise during language comprehension, and if this measure is reliable on the individual level when collected during different tasks. Then we examine whether $1/f$ noise mediates the effect of age on neural indices of accurate prediction of words during discourse comprehension, i.e., lexical prediction.

1.1. The Neural Noise Hypothesis of Aging

Neural noise has been defined as random, background electrical fluctuations within the central nervous system (Hong & Rebec, 2012; Li, Lindenberger, & Sikström, 2001; Serletis et al., 2011). Noise can be considered by comparison with the strength of the signal for relevant, or actively processed, information; a nervous system is noisy if the ratio of signal strength to random background noise is low (signal detection theory in Nevin, 1969; reviewed in Swets, 2014). Noisy systems may emerge when connections between neurons are weakened or diffuse as a function of reduced arborization, neuronal loss, or inconsistent inhibition (Cremer & Zeef, 1987). The brains of older adults often show these types of losses and changes across neural connections (e.g., Cabeza, Nyberg, & Park, 2016; Fjell & Walhovd, 2010; Raz et al., 2005), underlying a long-held hypothesis (Crossman & Szafram, 1956) positing that the effective signal-to-noise ratio in neuronal networks decreases with age.

For decades, reaction times to degraded stimuli were the primary means by which researchers quantified neural noise (e.g., Creemer & Zeef, 1987; Salthouse & Lichty, 1985; Welford, 1981). However, behavioral measures may not accurately address connections in neural networks, and may only reflect age-related degradation in peripheral sensory systems (i.e, as opposed to cortical neural noise). An alternate method may be to measure neural noise directly and non-invasively using the electroencephalogram (EEG). Oscillatory neural activity recorded at the scalp is thought to arise from dynamic communication across ensembles of neurons, and a number of researchers have proposed that these oscillations measure synchrony in neuronal firing (e.g., Fries et al., 2007; Miller et al., 2014; Voytek & Knight, 2015). Recent studies have further indicated that population-level neuronal spiking correlates with oscillatory activity due to generalized broadband activation, as opposed to oscillations specific to any particular frequency band (e.g., Kreiman et al., 2006; Manning, Jacobs, Fried, & Kahana, 2009; Miller et al., 2007). In other words, neural noise may be reflected in the distribution of neuronal activation (or the power spectral density, PSD) across the frequency spectrum.

In order to test this hypothesis, Voytek et al. (2015) used EEG to investigate PSD in young and older adults. If, as suggested by the neural noise hypothesis, older adults have less synchronized or less simultaneous neuronal spiking relative to younger adults, this should be observed in the distribution of spectral power across frequencies. The characteristic distribution of EEG data in the frequency domain is inversely proportional (He, 2004; Miller, 2010; Voytek et al., 2015), such that a linear relationship can be approximated by calculating the log of the PSD. Voytek and colleagues showed that the slope of this linear relationship can serve as a measure of 1/*f* *neural noise*[1], with more power at low frequencies relative to higher frequencies. In this study, older adults showed a flatter, less negative 1/*f* slope than younger adults. As PSD slopes are predicted to flatten when spiking activity is decoupled from oscillatory synchronization (Freeman & Zhai, 2009), these differences in 1/*f* neural noise have been interpreted as reflecting age-related declines in population-level synchrony across neuronal networks (Hong & Rebec, 2012; Podvalny et al., 2015; Voytek & Knight, 2015).

Voytek and colleagues (2015) found 1/*f* neural noise was higher for older adults performing a visual working memory task. In the present study, we examined whether similar age differences in 1/*f* noise could be observed during two language comprehension tasks. In addition to examining the effect of age on 1/*f* noise, we compared 1/*f* noise levels between two language tasks within individuals. In the first task (Comprehension Paradigm), participants were instructed to read single sentences for comprehension, while in the second task (Prediction Paradigm), participants were asked to try to predict the last word of a two-sentence passage. If 1/*f* noise represents a robust and reliable individual difference measure, we should observe strong correlations within subjects independent of differences in cognitive demands.

Finally, as Voytek et al. examined effects of 1/*f* neural noise on behavioral accuracy in their working memory task, this study tests if 1/*f* noise would similarly influence event-related neural responses during lexical processing. Specifically, we tested the hypothesis that age and neural network dynamics affect anticipatory processing.

1.2. Neural Noise and Predictive Processing

Current approaches in cognitive neuroscience emphasize the role of active, top-down mechanisms in the processing of incoming sensory stimuli (e.g., Clark, 2013; Friston, 2005; Hinton, 2010). These models suggest that the brain proactively generates expectations for upcoming information, compares real-world input with these internally held expectations, and adjusts accordingly. Such generative models of anticipatory processing – or *prediction* – are thought to have vast explanatory power across cognitive domains, and therefore have become an increasingly popular assumption of computational networks modeling neural dynamics (e.g., Dayan, Hinton, Neal, & Zemel, 1995; Jaeger & Haas, 2004; Maloney & Mamassian, 2009). However, very little evidence exists to link prediction to specific neural activation patterns.

[1]1/*f* noise, alternately known as *flicker* or *pink nose*, is defined as electrical activity associated with current flow in systems with few charge carriers, such as neurons (e.g., Hooge & Gaal, 1971; Stevens, 1972). 1/*f* neural noise has been observed in mammalian neural circuits since Verveen and Derksen (1965).

Emerging frameworks for anticipatory processing have described the brain as a Bayesian "prediction machine", or a network that distills statistical regularities from environmental stimuli and uses these statistics to make predictions about future events (Bastos et al., 2012; Clark, 2013; Friston, 2010). The predictive brain probabilistically generates models for upcoming information, and is believed to pre-activate those models when information is highly expected (i.e., when the environment strongly supports presentation of a specific stimulus). In order for prediction to be both efficient and generalizable across sensory and cognitive domains (i.e., unifying; Friston, 2005), top-down processing must be a fundamental architectural feature of neural organization. One explanation for neural encoding of prediction suggests that anticipatory mechanisms are embedded in spatio-temporal relationships across neuronal populations (Engel, Fries, & Singer, 2001). This temporal binding model postulates that higher-order brain dynamics modulate synchronous timing of neural firing. In other words, top-down information (e.g., expectations, goals, and attention) influences the size, strength, and cohesive firing of neural assemblies activated for expected input. If so, synchronous firing should be enhanced during prediction. Recent evidence shows that synchronous oscillatory activity in the brain is associated with the presentation of predictable, as opposed to unpredictable, stimuli (reviewed in Engel, Fries, & Singer, 2001; Arnal, Wyart, & Giraud, 2011; Doelling, Arnal, Ghitza, & Poeppel, 2014; Samaha, Bauer, Cimaroli, & Postle, 2015). In order for networks to show neural synchrony, stable and coherent networks must be established in the brain (Fries, 2005), and so we propose a corollary: prediction is enhanced for individuals with more synchronous neuronal networks.

In the present study, we test this hypothesis by examining the effects of age and $1/f$ neural noise on ERP indices of predictive processing during language comprehension.

1.3. Effects of Age and Noise on Prediction during Language Comprehension

ERP studies of lexical prediction typically examine effects of manipulating *cloze probability*, or the likelihood that a word will complete a given context[2] (reviewed in Kutas & Federmeier, 2011). Effects of cloze probability have primarily been reported to modulate the amplitude of two ERP components: the N400 and, more recently, the post-N400 positivity (PNP). The N400 is a negative deflection that is maximal over posterior electrode sites between 300 to 500ms after a word is presented. The amplitude of the N400 is reduced when comprehenders process high cloze (highly predictable) relative to low cloze (unpredictable) words in sentence or discourse contexts (reviewed in Swaab, Ledoux, Camblin, & Boudewyn, 2012). The N400 effect is thought to index neural facilitation when words are highly expected or pre-activated. The PNP is maximal to low-cloze continuations over frontal electrode sites between 600–900ms (reviewed in Delong & Kutas, 2016; Van Petten & Luka, 2012). The PNP is thought to reflect costs of resolving an unexpected word with the prior discourse, or costs associated with updating the discourse representation with new information. Modulations of the N400 and PNP as a function of critical word predictability are found both as a function of if critical words were actually accurately

[2]For example, for the sentence: *You could tell he was angry from the tone of his…*, the most predictable and therefore highest cloze completion is *voice*. An example of an unpredictable, low cloze competition is *violin.*

predicted by the reader, or were plausible given the preceding context. An ERP paradigm developed by Brothers and colleagues (2015) allows us to observe separate N400 and PNP effects for prediction accuracy and contextual plausibility (independent of prediction accuracy, henceforth referred to as effects of *context*).

In the Brothers et al. study, participants were asked to try to predict the last word of moderate cloze (40–60%) two-sentence passages and, at the end of each passage, to report whether the passage-final word matched the identity of the word they had predicted. The recorded EEG was sorted in different bins for accurately predicted and inaccurately guessed words. A subset of the passages presented in this study ended in low-cloze (0–7%) completions, and readers nearly always reported inaccurately guessing these unpredictable items. By comparing ERP in three conditions (accurately predicted moderate-cloze, inaccurately predicted moderate-cloze, and inaccurately predicted low-cloze items), Brothers et al. (2015; see also Brothers et al., 2017) found separable N400 and PNP effects of accurate prediction and contextual support (i.e., cloze probability independent of prediction accuracy). These components were larger in amplitude when the reader's prediction was incorrect and when the critical word was incongruent given the preceding context. Using this paradigm, Dave et al. replicated this pattern of results in older adult readers (Dave et al., under review), further findings that older adults had reduced effects of prediction accuracy and contextual support on the N400, while PNP effects were not modulated as a function of age. In the current study, we examined whether separate ERP measures of prediction accuracy and contextual support correlated with individual estimates of $1/f$ neural noise, and if noise contributed uniquely to age-related changes in amplitudes of ERP effects.

2. Results

2.1. 1/f Neural Noise across Age in Comprehension and Prediction Paradigms

We generated linear regressions modeling the relationship between frequency and log-based PSD, and analyzed the slopes ($1/f$ neural noise, or Noise) emerging from these analyses. Significant differences in Noise were observed between older and young adults on both tasks (Figure 1A). Younger adults had significantly steeper slopes than older adults (comprehension: $t(46) = 5.10$, $p < .001$; prediction: $t(46) = 3.51$, $p < .001$ for paired two-tailed t-tests, replicating the result of similar analyses in Voytek et al., 2015). Regression analyses provided good fit of the data in both age groups and tasks (rs > .70), indicating linear modeling of the data is well motivated.

In order to address whether Noise was similar between tasks, we first examined the frequencies for which age-related differences were significant. In the Comprehension task, significant age differences emerged across the entire 2–25Hz scale, excluding a subset of the alpha range (7–12.3Hz, p range: .12 to .44). Power decreased with age at lower frequencies (2–7Hz, high delta and theta), but increased with age at higher frequencies (beta). In contrast, significant age differences only emerged in a higher, primarily beta frequency range in the Prediction task (13.3–25Hz). As in the comprehension task, older adults had high power than younger adults at higher frequencies (ps > .01).

Next, we examined topographic correlations between age and Noise, to observe where age-related differences in 1/f neural noise were most pronounced across the scalp (Figure 1B). In the Comprehension task, age differences were found over much of the scalp, with the strongest age correlations emerging over central electrode sites. While correlations between age and Noise were generally reduced for the Prediction relative to the Comprehension task, these differences were not significant (whole head: $Z = 1.21$, $p = .23$). As displayed in Figure 2B, task differences in Noise-age correlations were only significantly over frontal electrode sites (comprehension task average: $r = .598$, prediction task average: $r = .233$, $Z = 2.15$, $p = .03$).

As Noise varied as a function of language task across both frequency and topography, we aimed to determine if participants showed intra-individual reliability (i.e., if slope measured across the entire scalp correlated for both tasks). 24 older adults performed both Comprehension and Prediction tasks[3], and served as our test population for evaluating whether Noise was a reliable measure of individual difference. As displayed in Figure 1C, slopes were significantly correlated ($r = .819$, $p < .001$) between tasks for older adults, suggesting that Noise remains stable despite variable task demands.

2.2. ERP Analysis in the Prediction Paradigm

ERP waveforms are plotted in Figure 2 to display the effects of two conditions on discourse processing: accurate prediction (Prediction: unpredicted minus predicted moderate cloze targets) and contextual support (Context: unpredicted low minus unpredicted moderate cloze targets).

As seen in Brothers et al. (2015; 2017) and Dave et al. (under review), young and older adults showed separate negative deflections between 300–500ms for effects of Prediction and Context. These effects were maximal at the typical centro-parietal sites (as in Kutas & Federmeier, 2011; Swaab, Ledoux, Camblin, & Boudewyn, 2012). Both age groups also showed significant positive deflections between 600–900ms for effects of Prediction and Context. This post-N400 positivity (PNP) was maximal over frontal electrode sites (as in Brothers et al., 2015; 2017; Federmeier, Wlotko, Ochoa-Dewald & Kutas, 2007; Van Petten & Luka, 2012).

Older adults typically show delayed ERP effects relative to younger readers (e.g., meta-analysis in Kutas & Iragui, 1998), and in the present study we also observed delayed N400 and PNP effects in older relative to young adults in the Prediction Paradigm. Therefore, as described in Dave et al. (under review), ERP effects were measured over 100ms epochs centered on maximal peak amplitudes for each group. N400 effects were measured over a representative cluster of six centro-posterior electrode sites (CP1/2, P3/4, Cz, Pz), while PNP effects were calculated across a cluster of six frontal electrode sites (FP1/2, F3/4, AFz, Fz).

[3]Correlations between tasks were not calculated for young adults because two separate sets of young readers participated in the Comprehension and Prediction Paradigm tasks.

Mean N400 and PNP amplitudes measured in these epochs were entered into separate mixed-effects rANOVAs including the 2-level factors of Age (Young, Old) and Type (Prediction, Context). A significant main effect of Age emerged ($F(1, 70) = 44.68$, $p < .001$) for N400s but not PNPs ($F(1, 70) = 0.47$, $p = .50$), indicating that older adults had smaller N400 effects than young adults but age did not affect average PNP amplitude. For both N400 and PNP effects, there was no main effect of Type, indicating that there was no difference in the size of N400 or PNPs effects of Prediction and Context (N400: $F(1, 70) = 0.13$, $p = .71$; PNP: $F(1, 70) = 0.14$, $p = .71$). Further, no interaction was found between Age and Type (N400: $F(1, 70) = 2.01$, $p = .16$; PNP: $F(1, 70) = 0.03$, $p = .88$).

2.3. Mediation Analyses for Age, Noise, and ERP Effects

To assess the impact of age group and *1/f* neural noise on ERP waveforms, we investigated if ERP effect amplitudes were influenced by Age and Noise. N400 effects of both Prediction and Context were significantly reduced in older readers (ps < .001, Figure 3A), while PNP effects were not impacted by Age (ps > .5). Likewise, flatter 1/*f* slopes correlated with smaller N400 effects of both Prediction ($p < .001$) and Context ($p = .007$, Figure 3B), while no significant correlations were found for PNP effects. As both Age and Noise were predictive of N400 amplitudes, and Age correlated significantly with Noise ($R^2 = .240$, $F(1, 70) = 22.09$, $p < .001$), structural equation models were constructed to examine if the strength of the relationship between Age and N400 amplitudes was altered by the addition of Noise as a mediating variable (Figure 3C).

The Sobel test (Sobel, 1982) for indirect effects of mediation was used to determine the product of the coefficients of (i) the relationship between Age and Noise (i.e., independent and mediating variables) and (ii) the relationship between Noise and N400 effects after controlling for Age (i.e., mediator and dependent variables). We first generated independent models for the relationship between Age and N400s effects of Prediction and Context. We subsequently generated models that included Noise, in order to determine if Noise explained Age-related changes in N400 effect amplitudes.

Age significantly predicted the N400 effect of Prediction ($t(71) = 5.79$, $p < .001$) in a model generated without Noise, $R^2 = .324$, $F(1, 70) = 33.56$, $p < .001$. In a multiple regression analysis with both Age and Noise, the effect of Age on the Prediction N400 remained significant ($t(71) = 4.07$, $p < .001$) but was partially mediated by Noise (Sobel test statistic: 2.08, $p = .035$). In the presence of Age, Noise still significantly predicted Prediction N400 amplitude, $t(71) = 2.32$, $p = .02$. While Age alone explained 32% of the total variance in Prediction N400 amplitude, effects of Noise unrelated to Age explained an additional 5% of the variance, and this addition to model fit was significant.

Similar analyses were performed for effects of Age and Noise on Context N400. Age significantly predicted the N400 effect of Prediction ($t(71) = 5.30$, $p < .001$) in a model generated without Noise, $R^2 = .287$, $F(1, 70) = 28.12$, $p < .001$. With the addition of Noise to the model, the effect of Age on Prediction N400 remained significant ($t(71) = 4.32$, $p < .001$) and Noise was not found to mediate this relationship (Sobel test statistic: 0.58, $p = .565$). Noise was not predictive of Context N400 in the presence of Age, $t(71) = 0.58$, $p = .56$, and only 0.3% additional variance was explained by effects of Noise unrelated to Age in this model.

In addition to mediation models, we conducted two additional sets of analyses. As observed above, age-related differences Noise across the Prediction paradigm were primarily driven by increased power in the beta range (14–25Hz) for older adults. We therefore examined whether age-related differences in beta activity correlated with N400 amplitudes, to assess if correlations between Noise and N400 amplitudes were driven by beta power. However, average power in the beta band was not significantly correlated with either prediction accuracy ($r = .038$, $p = .10$) or contextual support ($r = .007$, $p = .47$) effects on the N400.

Secondly, we investigated if Age significantly moderated the effect of Noise on N400 amplitudes, to test if different relationships between Noise and N400 effects emerged in each age group. However when entered alongside Age and Noise, the Noise by Age interaction was not significantly predictive of N400 effects of either Prediction ($t(71) = -0.02$, $p = .99$) or Context ($t(71) = 0.84$, $p = .40$).

3. Discussion

Consistent with previous findings, the current study demonstrates that $1/f$ neural noise reliably changes as a function of aging. Across both studies, slopes of the $1/f$ function flattened with advanced age, showing that this marker can be observed in EEG recorded in tasks with different cognitive demands. Several computational models (Freeman & Zhai, 2009; Manning et al., 2009; Miller et al., 2007) have suggested that this broadband measure of $1/f$ noise may relay the degree to which neural networks are synchronized in their firing, proposing that observed $1/f$ noise differences may reflect neuronal desynchronization in aging (i.e., neural noise hypothesis, Crossman & Szafram, 1956). Recent *in silico* modeling in rats and macaques (Gao et al., 2017) further demonstrate5 that power spectral density (and thereby $1/f$ neural noise) may not only track firing synchrony, but also the spatial and temporal contributions of excitatory and inhibitory (i.e., glutamate and GABA) synaptic inputs onto neuronal populations. As this measure of noise increases in older adults across a number of cognitive tasks (e.g., the two in the current study, Voytek et al., 201; Leenders et al., 2018), synchronicity *and* excitation-inhibition balance in neural networks may change as a byproduct of typical aging.

While young adults typically had more negative noise slopes than older adults, slope ranges showed some overlap between groups. Therefore, while neural noise correlated with age, $1/f$ slopes were not entirely explained by age group differences. We observed age effects on noise slopes in each task, and found two key results. First, age correlated most strongly with $1/f$ slopes in central regions of the scalp for both tasks. Interestingly, the addition of the prediction task resulted in a somewhat shifted topography for age by slopes correlations, suggesting that age differences in neural activation patterns are modulated by additional task demands (as seen in Gazzaley et al., 2008; Klostermann et al., 2007). Second, we correlated noise slopes across language tasks in the population of older adults studied in the current experiment. Whole head $1/f$ slopes strongly correlated despite both different reading goals and different topographies between tasks, reflecting that noise is a consistent and characteristic measure of the individual. These results imply that 1/*f* noise may serve as a neural measure of individual differences in older cohorts. Between-task correlations in noise for young adults could not be calculated in the present study, as two groups of young adults participated in the two experiments. It will be important for future studies to examine whether similar 1/*f* noise correlations emerge in both age groups.

Expanding on the behavioral findings of Voytek and colleagues (2015), our study aimed to investigate whether the steepness of the 1/*f* slopes was correlated with ERP measures related to language processing. Our results show that N400 effects were modulated by this EEG-derived measure of noise, but PNP effects were not correlated with noise. Therefore, the effects of neural noise may be specific to certain language comprehension processes. N400 modulations are associated with facilitation of lexical-semantic processing when a presented word is accurately predicted (Prediction N400), or matches the meaning of the previous context independent of prediction accuracy (Context N400). In contrast, PNP amplitudes have been associated with "work" necessary to revise or update discourse representations (Brothers et al., 2015; Van Petten & Luka, 2012) following the presentation of unexpected words. Our findings suggest that these updating processes are less likely to be affected by neural synchrony. N400 activity is found to every word that is presented via RSVP, as a function of incremental surprisal and unfolding contextual information (Kutas & Federmeier, 2011). Thus it is likely that the 1/*f* noise measure partially reflects N400s across each sentence. Critically, however, our results show differential effects of 1/*f* noise on N400s associated with processing specific lexical expectations and those associated with integration of contextual fit information, suggesting activity across frequencies offers unique and partially explanatory contributions to specific components of the N400.

A key finding of the current study – that 1/*f* neural noise specifically influenced N400 effects of accurate lexical prediction – is largely consistent with Engel et al.'s (2010) proposal that neural network dynamics (specifically, population spiking synchrony) underlie the strength of predictions generated during anticipatory processing. Several studies have found that oscillatory activity in narrowband frequency ranges change prior to presentation of predictable, as opposed to unpredictable, stimuli during language comprehension (Lewis & Bastiaansen, 2015; Rommers et al., 2016; Vignali et al., 2016). Critically, these studies have emphasized the "frequency [band] specificity" of these findings (Bastiaansen & Hagoort, 2016, p. 190). However, our results indicate that observed age-related differences in spectral power in specific frequency bands (i.e., beta) did not correlate with N400 effects of predictive accuracy, and therefore cannot explain how 1/*f* neural noise mediates age-related changes in this neural index of prediction. Therefore, our current study re-affirms Voytek et al. (2015)'s argument that researchers benefit from studying the power spectrum as a "unified statistical representation of the signal" (p. 13262).

To our knowledge, no prior studies have examined the role of broadband EEG activity in predictive processing. Furthermore, our study is the first to find individual differences in predictive processing as a function of neural noise and aging. This EEG-derived measure represents a readily available, non-invasive index of neural synchrony that can be observed at the single subject level to predict individual differences in behavioural and neural outcomes. There is broad potential for future studies in applying this technique in understanding individual differences in cognitive processes, both in typical populations and in individuals affected by neural disease (i.e., Alzheimer's). However, it remains to be determined whether an accurate index of 1/*f* noise can be obtained over shorter time scales, or in resting state. Additional research will be necessary for determining the recording characteristics that will optimize 1/*f* neural noise measurement for laboratory and clinical investigation.

It is particularly important to note that in both Voytek et al. and the current study, 1/*f* slopes did not mediate all behavioral or neural measures showing age-related declines (e.g., no mediation was found for response times in Voytek et al., or N400 effects of Context in the current study). Instead, noise mediated specific age effects of (i) accurate behavioral responses and (ii) neural effects of prediction accuracy. Friston (2005)'s foundational model of predictive processing defines accuracy as a minimization of prediction error, yielding reductions in bottom-up neural activity when a comprehender has pre-activated (predicted) a representation of the expected stimulus. This conceptualization suggests that neural noise slopes may specifically reflect the maintenance of top-down mechanisms that allow comprehenders to generate expectations and/or pre-activate specific stimuli (as posited by Engel et al., 2010; Clark, 2013). It will be critical for future research to address how neural synchrony modulates top-down processing. Computational and theoretical models have suggested 1/*f* noise may dynamically influence effortful processing (Grigolini et al., 2009), representation formation (Gilden, 2001), and strategic shifting (reviewed in Wagenmakers, Farrell, & Ratcliff, 2004) – all of which have been suggested to underlie predictive processing across the lifespan (i.e., Clark, 2013; Federmeier, 2007; Kuperberg & Jaeger, 2016).

Importantly, the 1/*f* noise component reflects broadband power measured *prior* to critical word onset. We generated the N400 Prediction effect by comparing across trials for which readers self-reported that they "accurately" or "inaccurately" predicted the final/critical word; however, the sentences themselves had equal offline cloze probability for target words (i.e., were all moderate-cloze trials). In other words, contextual informativeness does not differ between "accurate" and "inaccurate" moderate-cloze prediction conditions, and the only distinction between these conditions is whether the reader predicted the final word. Broadband activity differences preceding this point may therefore reflect strongly-held predictions, such that words readers marked as "accurately predicted" were highly expected. In contrast, contextually-similar trials that were marked as "inaccurate predictions" may contain not only trials where strong predictions were made for likely but unpresented words, but also a number of trials with weak or absent predictions. Thus differences in broadband activity preceding sentence-final words may reflect differences in anticipatory mechanisms preceding accurately as compared to inaccurately predicted words.

Because N400 effects of Context were not linked to 1/*f* neural noise after controlling for age, activation patterns required for effective contextual processing are very likely distinct from those underlying predictive mechanisms (as seen in oscillatory analyses performed by Rommers et al., 2016). Importantly, no evidence emerged to suggest differential involvement of 1/*f* noise in predictive processing in young and older adults. Instead, we posit that similar neural mechanisms for lexical prediction (Kuperberg & Jaeger, 2016) are recruited by both young and older adults. Benefits of top-down information are likely guided by both neuronal spiking synchrony, as well as sources of variance that are related to age but may be independent of $1/f$ neural noise.

What these sources of variance may be is an open question, but neural noise as measured by EEG $1/f$ power alone may not fully describe how noise modulates neural network dynamics. Some researchers have posited that inter-trial variability may also capture age-related decline in signal fidelity, and have successfully linked aging to inconsistency in behavioral responses (Hong & Rebec, 2012; Hultsch & MacDonald, 2004; Lovden, Li, Shing, & Lindenberger, 2007), as well as fMRI (D'Esposito et al., 1999) and oscillatory phase coherence (Papenberg et al., 2013). Further, recent evidence (Payne & Federmeier, 2017) has emerged to suggest that contextual processing may be dependent on intra-individual, trial-to-trial variability in ERP activity. Taken together with the results of the current study, Payne and Federmeier's results indicate that effects of prediction accuracy and contextual support may both be modulated by synchrony, but that these measures represent distinct subcomponents of neural noise. Future research would benefit from incorporating elements of both network-level spiking synchronization (i.e., $1/f$ neural noise) and trial-specific neural activity (i.e., inter-trial variability) in gauging the mechanisms underlying language processing in young and older adults.

4. Methods

4.1. Participants

4.1.1. Comprehension Paradigm—EEG data were collected from 24 young adults (19 females; mean age: 19.5; range: 18 to 28) and 24 older adults (14 females; mean age: 72.0 years; range 64 to 79). All participants were native English speakers with normal or corrected-to-normal vision and no known history of psychiatric or neurological disorders, head trauma, or neuro-active prescription medication. All participants were right-handed, as assessed by self-report and the Edinburgh Handedness Inventory (Oldfield, 1971). Both groups provided 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 analyses due to excessive artefacts in EEG recordings.

4.1.2. Prediction Paradigm—EEG data were collected from 36 new young adult participants (19 females, mean age: 20.5; range: 18 to 33). The same 24 older adults were tested on the prediction paradigm, and 12 new older adult participants were also included (total group: 21 females; mean age: 70.8 years; range 64 to 79).[4] All participants were consented to the same criteria described above. Data from two additional young adults and three additional older adults were excluded from the analyses as a result of excessive artefacts in EEG recordings.

[4]Dave et al. (under review) reports results from Prediction Paradigm ERP analyses of 48 of these 72 subjects. An additional 24 subjects (12 young, 12 older adults) were tested for the current Prediction Paradigm findings, as well as those participants tested on the Comprehension Paradigm.

4.2. Stimuli and Procedure

4.2.1. Comprehension Paradigm—Participants read 100 experimental sentences, presented via rapid serial visual presentation (RSVP) with a stimulus-onset asynchrony (SOA) of 600ms. Participants were instructed to read each sentence for comprehension, which was tested by manual response to true/false statements following 25 percent of trials.

4.2.2. Prediction Paradigm—Participants read 180 two-sentence discourse passages (detailed in Brothers et al., 2015). Sample stimuli for this paradigm are presented in Table 1.

The first sentence of each passage was presented all at once, and the second sentence was presented via RSVP (SOA: 600ms). Participants were instructed to try to use the discourse context to predict the final word of each passage, and to manually indicate whether the actually presented passage-final word matched their expectations. Readers were informed that there were no “correct” predictions for any passage.

Of the 180 passages, 120 were constrained such that the final word was very likely to be one of two possibilities (cloze for each possibility: 40–60%, average: 51%). For these moderate cloze passages, the passage-final word was equally likely to be accurately or inaccurately predicted by the reader (see Table 1). 60 additional passages were presented that were similarly constrained toward two likely target completions; however, the final word presented at the end of these passages was instead a low cloze, improbable item (low-cloze: 0–7%, average: 0.9%), such that readers were likely to indicate that target word was not predicted.

4.3 EEG Recording

EEG data was recorded using SCAN (Compumedics Neuroscan), and processing and analysis was performed using Matlab (The MathWorks, Natick, MA) and EEGLAB toolbox. EEG was recorded during both tasks with 29 tin electrodes mounted in an elastic cap (ElectroCap International). Additional electrodes were attached below and on the outer canthi of the eyes in order to capture blinks and other eye movements. Electrode impedances were kept below 5kΩ, and the EEG signal was amplified with a Synamps Model 8050 Amplifier (bandpass cutoffs: 0.05 – 100Hz). The signal was continuously digitized at a sampling rate of 250Hz. All channels were initially referenced to an electrode placed over the right mastoid and later re-referenced to the average of left and right mastoids.

After EEG recording, independent components analysis (ICA) was used to decompose EEG responses into subcomponents with fixed scalp distributions and independent time courses. After ICA, eye blink components were removed, and single-trial waveforms were screened for amplifier blocking, muscle artifacts, and horizontal eye movements.

4.4. EEG Analysis for 1/*f* Neural Noise

For data collected during the Prediction Paradigm, EEG was epoched to exclude the following: all times in which participants were on breaks (i.e., between passage presentations), the first sentence of each passage (i.e., when participants were encouraged to move their eyes freely over the entire sentence, presented en masse), and passage-final words. For data collected during the Comprehension Paradigm, EEG was similarly epoched to exclude all times in which participants were on breaks, as well as sentence-final words. $1/f$ noise was calculated for EEG collected during sentences presented via RSVP, from 300ms preceding presentation of the first word to 300ms after presentation of the second-to-last (i.e., $n - 1$) words of experimental stimuli.

We replicated the broadband power spectral density (PSD) analyses for $1/f$ neural noise originally performed by Voytek et al. (2015). Voytek and colleagues estimated slope from EEG in the 2–25Hz PSD range, excluding the alpha range (7–14Hz). High frequency activity (gamma band; 25–100Hz) was excluded from scalp recordings due to likely overlap with face and eye muscle activity (e.g., Voytek et al., 2010; Luck, 2005). Alpha activity was excluded from slope analyses because oscillations in this frequency band are inconsistent with broadband local-field potential patterns (i.e., alpha activity is believed to be representative of non-broadband activity; Manning et al., 2009; Miller, 2010; Miller et al., 2014).

The fast Fourier transform (FFT) power spectrum was calculated at each channel for each participant (*fourieeg.m* function in EEGlab, wherein PSD was estimated using N 1500ms time windows with 50% overlap between 2 and 25Hz). PSD is thought to be inversely proportional with frequency (Miller, 2010), and therefore PSD was log transformed. By using $\log_{10}$PSD, linear regressions generated between frequency and PSD yielded a representative slope of the power spectrum (i.e., $1/f$ neural noise).

4.5. ERP Analysis for the Prediction Paradigm

ERP processing was performed using Matlab with the EEGLAB toolbox and ERPlab plugin (Luck, 2005). ERP analyses were performed over the final words of passages over epochs of 1500ms, starting 300ms before the onset of the critical target items. ERP waveforms were sorted into three conditions: (i) accurately predicted moderate cloze completions, (ii) inaccurately predicted moderate cloze completions, and (iii) inaccurately predicted low cloze completions. (Very few (<10% per subject) of low cloze words were marked as accurately predicted, and therefore waveforms were not averaged for this condition.)

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Highlights

- EEG-derived 1/*f* neural noise varies reliably as a function of age
- Noise correlates strongly within subjects across tasks
- Noise predicts N400 effects of lexical prediction in young and older adults
- Noise does not predict other N400 effects, or other ERP effects
- Specific contributions of synchronous neural firing to predictive mechanisms

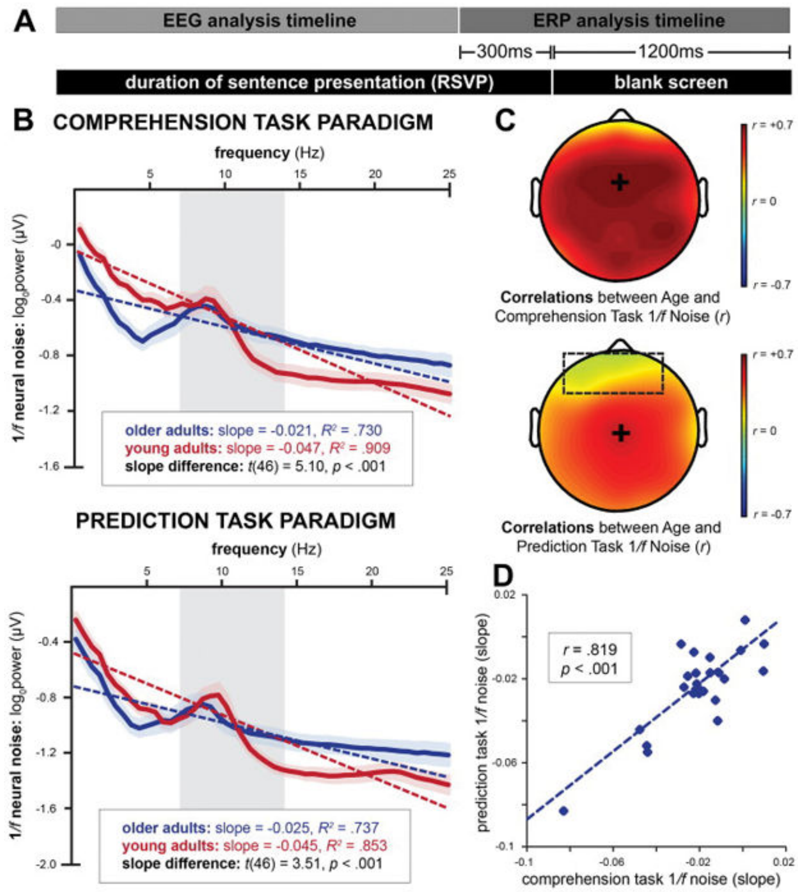

Figure 1.

1/*f* neural noise across task and age. (**A**) EEG was recorded during and briefly following rapid-serial visual presentation (RSVP) of sentences in both Prediction and Comprehension Paradigms. EEG recordings used to calculate 1/*f* noise were collected until 300ms prior to the end of each sentence, immediately followed by non-overlapping EEG recordings that were later averaged to generate ERP waveforms to critical words. (**B**) 1/*f* neural noise was estimated for both paradigms from the slope (dotted lines) of the power spectrum across frequency (2–25Hz, plotted above with 95% confidence intervals), excluding alpha frequency (7–14Hz, shaded). (**C**) Correlations between Age and 1/*f* slopes are plotted topographically. Correlations were maximal over central electrode sites for both paradigms (addition signs). Age correlations with neural noise were not significantly different as a function of task, but topographic differences between tasks emerged over frontal electrode sites (dotted outline). (**D**) 1/*f* slopes were strongly correlated between tasks for older readers.

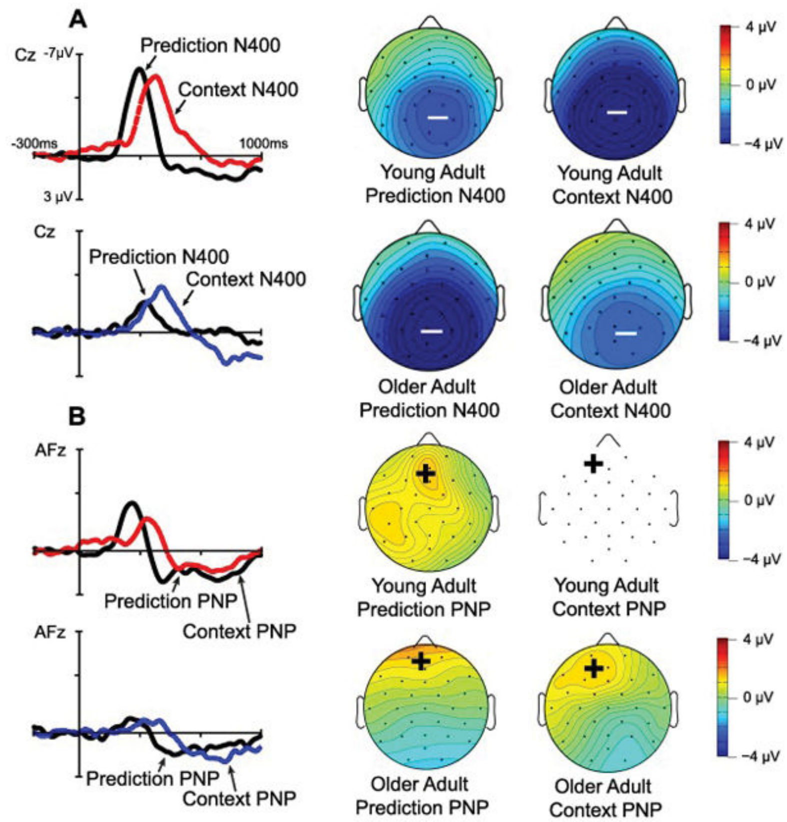

Figure 2.

ERPs in the Prediction Paradigm. ERP difference waveforms were generated for the effects of Prediction (unpredicted minus predicted words in moderate cloze passages) and Context (unpredicted low cloze minus unpredicted moderate cloze critical words), plotted at a frontal medial (AFz) and central (Cz) electrode site. Effects of Prediction and Context are plotted for young and older adults for N400 effects (**A**) and PNP effects (**B**), alongside topographic plots (right) indicating where effects were maximal in 100ms centered maximal epochs.

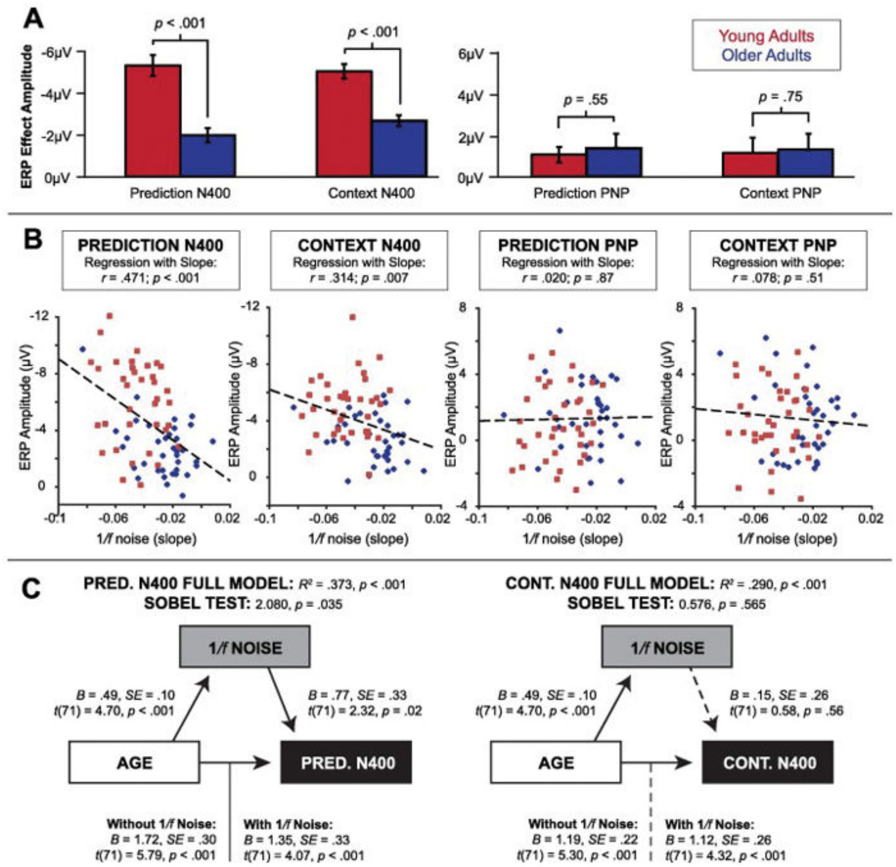

Figure 3.

Age, $1/f$ noise, and ERPs. N400 amplitudes for Prediction and Context were reduced in older readers (blue) relative to younger adults (red, **A**), but no significant effects of age were found for either of the PNP effects. (Error bars indicate standard errors (SEM).) $1/f$ neural noise was significantly correlated with amplitudes of both N400 effects (**B**), but not with the PNP effects. A mediation model generated for the Prediction N400 (**C**, left) shows that $1/f$ neural noise partially mediated age-related reductions in the Prediction N400. In contrast, a similar mediation analysis performed for the Context N400 (**C**, right) shows that $1/f$ neural noise is not predictive of Context N400 amplitudes after controlling for age, and does not mediate age-related reduction of the Context N400 (dotted lines).

Table 1

Sample experimental stimuli for the Prediction Paradigm.

Condition	Sentence 1	Sentence 2	Reader Expectation	Actual Presentation
Moderate cloze, Accurately Predicted	While at the bar, Theresa glanced at the handsome man's ring finger.	Her eyes widened when she found out that he was…	Married	**Married**
Moderate cloze, Inaccurately Predicted	While at the bar, Theresa glanced at the handsome man's ring finger.	Her eyes widened when she found out that he was…	Single	**Married**
Low cloze, Inaccurately Predicted	While at the hospital, Theresa read her son's medical report.	Her eyes widened when she found out that he was…	Sick	**Married**