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How the healthy ageing brain supports semantic binding during language comprehension

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Abstract

Semantic binding refers to constructing complex meaning based on elementary building blocks. Using EEG, we investigated the age-related changes in modulations of oscillatory brain activity supporting semantic binding. Young and older adult participants were visually presented two-word phrases in a semantic binding (e.g. swift *horse*) vs. no semantic binding context (e.g. swrfeq *horse*). We found that the oscillatory brain activity associated with semantic binding significantly differed between healthy older and young adults. Specifically, in young adults we found a semantic binding signature in the low-beta range centred around the onset of the target word (i.e. a smaller low-beta *in*crease for binding relative to no binding), while in healthy older adults we found an opposite pattern about ~500ms later in the low- and high-beta range (i.e. a smaller low- and high-beta *de*crease for binding relative to no binding). We interpret the different and delayed oscillatory signature for semantic binding in healthy older adults to reflect that they are relying on different mechanisms to integrate word meaning into their semantic context.

Keywords: semantic integration, language comprehension, healthy ageing, alpha, beta oscillations

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Introduction

Healthy ageing is accompanied by decline across a number of cognitive domains, such as your memory for events and the speed with which you process information (Salthouse, 1996; Waters & Caplan, 2005). Language is a crucial aspect of cognition, but the picture of how ageing affects language is a complex one. Older adults get better at some aspects of language, such as knowing more words (Brysbaert et al., 2016), while other skills clearly deteriorate, for example, accessing all the word-related information you need for production (Hardy et al., 2020; Segaert, et al., 2018). At the same time, many other language abilities, including sentence comprehension, appear relatively unchanged by healthy ageing (Peelle, 2019; Shafto & Tyler, 2014). For example, sentence comprehension performance has been demonstrated to be comparable between older and young participants, unless the stimuli are presented at a rapid rate (Tun, 1998; Wingfield et al., 2003) or with background noise (Tun, 1998). The complex behavioural picture for language function is difficult to reconcile with the widespread structural decline in language-relevant brain regions (Antonenko et al., 2013). Language performance in older adults is likely supported therefore by different functional neural processes from those in young adults (Peelle, 2019). The aim of the current EEG study is to investigate the differences between healthy older and young adults in the neural processes involved in semantic binding.

When we combine words, the meaning of an individual word (e.g. flat) can be altered by the meaning of a following word (e.g. flat tire vs. flat note) such that the combined meaning is more than the mere sum of its parts (Hagoort et al., 2009; Keenan, 1979). This illustrates the unique and expressive power of language: we have the ability to combine words in novel ways to create sentences. In other words, language users construct complex meaning from more elementary semantic building blocks (Hagoort, 2020; Hagoort et al., 2009). This ability forms the basis for communication and social interactions. Understanding the meaning of a multi-word utterance requires a process we refer to here as semantic binding. Lexically retrieved information about single words needs to be integrated into a representation of a multi-word utterance. This process has also been referred to as merge (Chomsky, 1995; Zaccarella & Friederici, 2015) or unification (Hagoort, 2005).

Neuroimaging studies employing fMRI have been able to provide a wealth of information about the location of brain areas likely associated with semantic binding in young adults. Previous investigations have found evidence that semantic binding requires the exchange and

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integration of information in a large network of frontal and posterior areas, including left inferior frontal gyrus, bilateral superior and middle temporal gyri, anterior temporal lobe and angular gyri (Baggio & Hagoort, 2011; Lyu et al., 2019; Menenti et al., 2011; Pylkkanen, 2019; Tyler & Marslen-Wilson, 2008).

The functional neural characteristics supporting specific language functions in healthy older adults, have often been found to differ from those in young adults (Antonenko et al., 2013; Peelle, 2019; Shafto & Tyler, 2014; Tyler et al., 2010; Wingfield & Grossman, 2006). With age, structural changes occur in language-relevant brain regions. In the context of these structural changes, it would be unlikely that successful performance in older adults is achieved with identical neural processes as in young adults (Peelle, 2019). Generally, the literature shows a more widespread pattern of activity in healthy older adults relative to young adults (e.g., Cabeza et al., 2002; Davis et al., 2008). Different views exist on how to interpret these age-related changes in brain activity: the appearance of more diffuse activity in older adults may reflect a general decline in neural efficiency (i.e. dedifferentiation), alternatively (though not mutually exclusive) increased engagement of brain regions may reflect focused recruitment as a means to compensate for neurocognitive decline (i.e. compensation) (Wingfield & Grossman, 2006).

One limitation of fMRI is the slow time course of the hemodynamic response (1.5-5 seconds) which limits what information it can provide about 'when' the specific neural processes involved in semantic processing are occurring. While EEG as a neuroimaging tool does not have the spatial resolution of fMRI, it does provide a real-time window into the neural activity underlying cognition. EEG studies investigating how the brain supports semantic comprehension, have primarily looked at event-related brain potentials (ERPs) which represent brain activity phase-locked to the onset of words. These studies have consistently found that word meaning in young adults is integrated into the meaning of a larger multi-word utterance at around 400-500ms after the relevant word, as indexed by the N400 ERP (Kutas, Hillyard, 1980; Kutas & Federmeier, 2011).

Previous studies have also elucidated several relevant aspects of how older adults comprehend sentence-level meaning. Healthy older adults do extract and make use of contextual semantic information (Stine-Morrow et al., 1999), but there are differences (compared to young adults) with respect to when and how this happens. Sentential context manipulations (i.e. the strength of contextual constraint for sentence-final words) elicit

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reduced and delayed N400 effects for older (compared to young) adults (Federmeier & Kutas, 2005; Wlotko & Federmeier, 2012). Moreover, effects of message-level congruity on the N400 are delayed by over 200ms in older adults (Federmeier et al., 2003). Ageing also affects processing of compositional concreteness, i.e. processing of the second noun in a noun-noun pair, in function of whether the first was concrete versus abstract (e.g. alias-battle vs. skate-battle) (Lucas et al., 2019), further suggesting that there are age-related changes in compositional semantics in healthy older (compared to young) adults.

There may be multiple (not mutually exclusive) sources of the observed age-related changes in how the brain supports making use of contextual semantic information. Older adults may engage different functional neural processes to support semantic binding and maintain a message-level meaning representation while processing incoming information. In addition, older adults may be less able to use prediction mechanisms during language comprehension. Several studies have provided support for the latter (Federmeier et al., 2002; Wlotko et al., 2012). In the present study, we focus on the former: do healthy older and young adults engage different neural mechanisms for semantic binding?

The EEG signal contains oscillatory activity (i.e., rhythms) which are hypothesised to play a vital role in how the brain carries out cognition (Mazaheri, et al., 2018; Siegel et al., 2012). Investigating the oscillatory (i.e., spectral) changes in the EEG allows for capturing activity that is time-locked but not necessarily phase-locked to experimental events (i.e., the onset of words). Studies focusing at the spectral changes in the EEG have found that the exchange and integration of information required for semantic binding, involves modulations in the oscillatory power in the theta (~4-7 Hz), alpha (~8-12 Hz), and beta bands (~15-25 Hz) (for comprehensive reviews: (Meyer, 2018; Prystauka & Lewis, 2019; Weiss & Mueller, 2012)).

In the present study, we aim to investigate modulations in oscillatory brain activity during semantic binding in healthy older compared to young adults, using a minimal two-word phrase paradigm. We present target words (e.g. horse) in a semantic binding (e.g. swift horse) vs. no semantic binding context (e.g. swrfeq horse). In both cases, for the target word, retrieval of lexico-semantic information from memory takes place. However, only in the binding condition a complex meaning representation can be built for the phrase, based on the elementary building blocks of each individual word. Within the semantic binding condition we also manipulate whether the phrase is plausible. The computation for a two-word phrase forms the foundation of binding in the context of increasing complexity. Investigating

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elementary semantic binding by means of a minimal phrase paradigm offers the advantage of focusing on the binding process while minimizing contributions of other processes involved in sentence comprehension, such as working memory load and the ability to use predictions. This advantage is particularly salient when investigating age-related changes in how the brain supports online sentence comprehension, given that working memory and the ability to use predictions are also impacted by age. Bemis & Pylkkänen (2011) conducted one of the first studies with a minimal paradigm, and compared nouns in a minimal binding context (e.g. red boat) versus a wordlist condition (e.g. cup boat). This inspired many other studies to use similar designs (Bemis & Pylkkänen, 2013; Pylkkänen et al., 2014; Segaert, et al., 2018; Zaccarella et al., 2017; Zaccarella & Friederici, 2015). Poulisse et al., (2019, 2020) used this approach to investigate how healthy ageing impacts minimal syntactic binding. Although secondary, the use of this paradigm also allows an investigation of lexical retrieval effects (e.g. swift vs. swrfeq) so we will report these findings as well.

If previously observed age-related changes in making use of contextual semantic information are at least in part due to a change in how the brain supports semantic binding, then we expect to see different oscillatory signatures for healthy older versus young adults, in the semantic binding versus no semantic binding conditions.

Method

Participants

33 young adults and 32 healthy older adults took part in the study. However, 7 participants were excluded from the analysis due to: (a) excessive EEG artefacts recordings (N=4), and (b) being bilingual (N=3). The participants included in the analyses were 29 young adults (2 males, aged 18-24) and 29 healthy older adults (13 males, aged 63-84) (see Table 1 for more information). All participants were right-handed, British-English monolingual speakers with normal-to-corrected vision and no neurological or language impairments. All older adults scored above 26 out of 30 in the MOCA test (M = 27.79, SD = 1.01) (scores ≤ 26 suggest risk of mild cognitive impairment or dementia (Smith et al., 2007)).

The young adults were Undergraduate students from the University of Birmingham and took part in the study for course credits. The older adults were from the Patient and Lifespan Cognition Database and were compensated for their time with cash payments. Participants

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signed informed consent, which followed the guidelines of the British Psychology Society code of ethics and the experiment was approved by the Science, Technology, Engineering, and Mathematics (STEM) Ethical Review Committee for the University of Birmingham (Ethics Approval Number: ERN_15-0866).

There was no significant difference in the number of years spent in education between the younger and the older adults. In line with expectations, young adults outperformed older adults in processing speed (Weschler Adult Intelligence Scale-IV processing speed index), whereas older adults outperformed young adults on the National Adult Reading Test (Nelson, 1982). Surprisingly, older adults also outperformed young adults in the working memory tasks (i.e. the average combined score of the backward digit span and subtract 2 span tests) (Waters & Caplan, 2003), which could be attributed to young adults being less motivated when they were participating in the tasks (in line with similar findings reported previously: Heyselaar et al., (in press)).

Table 1. *Demographic and cognitive characteristics for young and older adult participants*

	Young adults (N=29)		Older adults (N=29)			
	M	*SD*	*M*	*SD*	*t-value*	*P*
Age (years)	19.5	1.5	73.6	5.8		
Years of education	14.52	1.5	15.45	3.08	-1.46	*.15*
Processing speed	81.48	11.57	65	13.17	4.97	*< .001*
NART	25.81	5.07	37.05	4.61	-8.82	*< .001*
Working memory	4.42	.66	4.97	.92	-2.62	*<.05*

Design, materials and task

We created a minimal language comprehension paradigm with two-word-phrases. Each phrase included two words, where the target word was always the second word. The design of the study, with example stimuli, is illustrated in Figure 1. We manipulated lexical retrieval (comparing real words to letter strings) and semantic binding (comparing the target word in a semantic binding context to a no semantic binding context). We were primarily interested in the effects of semantic binding, but since our two-word phrase paradigm allows examining the effects of lexical retrieval also, we report these effects below as well. Within the semantic

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binding condition, we furthermore manipulated whether semantic binding was plausible (e.g. swift horse) or implausible (e.g. barking horse).

Lexical retrieval (first word)	Semantic binding (second, target word)
lexical retrieval *e.g. swift*	semantic binding *e.g. horse*
no lexical retrieval *e.g. swrfeq*	no semantic binding *e.g. horse*

Figure 1. Example word-pairs in each condition.

To ensure participants paid attention to the word-pair stimuli throughout the experiment, we included questions about the word-pairs on a subset of the trials (22% of all trials). The questions asked "Did you just see [word pair]". There were no significant differences between young and older adults in response accuracy (young adults: mean = 94.83, SD = 0.5; older adults: mean = 96.48, SD = 0.2; t(42.109) = -1.557, p = .127) or reaction times (young adults: mean = 1718.78, SD = 503.64; older adults: mean = 1851.45, SD= 488.92; t(56) = -1.018, p = .313). All the participants scored higher than 80%. From this we can conclude that young and older adults paid close attention to the language stimuli as they were being presented to them throughout the experiment.

We verified our plausibility manipulation in an online rating study with 57 respondents. The online survey asked to rate the plausibility of the two-word phrases, where 1 = 'Completely implausible', 2 = 'Somewhat implausible', 3 = 'Somewhere in between', 4 = 'Somewhat plausible', and 5 = 'Completely plausible'. The plausibility ratings were significantly different for the plausible (M=3.87, SD=.29) and the implausible word-phrases (M=1.93, SD=.66); Welch's F(1, 101.65) = 526.36, p < .001.

In each condition, about half of the target words were animate, the other target words were inanimate. The exact trial distribution was as follows: inanimate-plausible (N=45), inanimate-implausible (N=46), inanimate-letter string (N=44), animate-plausible (N=42), animate-implausible (N=47), and animate-letter string (N=46). The list of plausible and implausible adjectives was matched for frequency (plausible mean = 28.16, implausible mean = 27.87), number of syllables (plausible mean = 1.74, implausible mean = 1.79) and length (plausible mean = 5.87, implausible mean = 5.64).

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Three versions of the experiment were created, where the same word-pairs were presented in different orders. Participants were randomly assigned to one of the three versions. The paradigm intended to present 60 attention-questions for each of the versions of the experiment. However, due to an error in creating the question lists, the number of questions differed slightly per version (either 61 or 62 questions). The questions were not used in any of the EEG analyses. A full stimulus list, each of the 3 versions of the experiment, with the exact attention questions asked, can be downloaded from https://osf.io/f8grv/.

Procedure and trial timing

We presented our experiment using E-prime 2.0. The presentation time of each element in the trial is depicted in Figure 1. The task consisted of 270 trials divided into 9 blocks. In between each block, we offered the participants a break.

Figure 2. Trial presentation of the minimal two-word phrase paradigm. The questions appeared in 22% of the trials.

Upon the start of the experimental session, participants were fitted with a 64-electrode EEG cap. Once the EEG set-up was finished participants sat in a sound proof booth 70 cm from the monitor where the computerised task took place. Participants were instructed to read in silence word-pairs (e.g., hollow table) appearing on the screen. They were told that from time-to-time they would see a question on the screen regarding the word-pair that they had just seen (e.g. Did you just read 'hollow table?'). Participants were able to indicate 'yes' or 'no' using a button box. Participants completed a practice block first to familiarise themselves with the paradigm (30 word-pairs, with 9 questions, which were different from the experimental stimuli), which was followed by the actual experiment. Following the computer task, participants completed Working Memory tests (i.e. the Backward digit span task and the subtract 2-digit span task) (Waters & Caplan, 2003), National Adult Reading Test (NART) (Nelson, 1982), and the Weschler Adult Intelligence Scale-IV processing speed

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index (Weschler, 2008). In addition, the older participants also completed the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005).

EEG recording

EEG was recorded using Waveguard caps containing 64 cap-mounted Ag/AgCI electrodes (10-20 layout, including left and right mastoids). Horizontal eye movements were measured by two electrodes placed on the outer left and right canthi. Vertical eye movements were recorded by two electrodes placed above and below right eye. The EEG recording was acquired with online reference to the CPz channel. The signal was amplified with the ANTneuro EEGosports amplifier system and recorded using EEGo software (Advanced Neuro Technology). The signal was obtained using a 30Hz low-pass filter, a 0.05Hz high-pass filter and a 500Hz sampling rate. Impedances were kept below 100 kΩ.

EEG analysis

The EEG pre-processing was performed using EEGLAB 14.1.2b (Delorme & Makeig, 2004) and Fieldtrip toolbox 2018-07-16 (Oostenveld et al., 2011). The data were epoched to the onset of the first word (-1.5sec to 4.4sec) and later offline re-referenced to the average of all of the channels, where the mastoid and bipolar electrodes were excluded from the re-referencing. EEGLAB was used for manual inspection and rejection of trials with non-physiological artefacts. The average number of removed trials was 26.34 (SD=21.93) per participant due to artifacts. Ocular artifacts were removed based on the scalp distribution using independent component analysis ("runica") in EEGLAB. The average number of removed components was 2.07 (SD=.81) for each participant. Channels TP8 and TP7 were removed before completing any analyses due to poor/ no signal from these channels across the participants.

Time-frequency representations of power

Time-frequency representations of power were performed using the Hanning tapers and the 'mtmconvol' method with a time window of 3 cycles per each frequency of interest (DT = 3/f) for every trial. The analysis included the frequency of interest of 2Hz to 30Hz in steps of

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1Hz, and the time of interest of -1.5 to 4sec in steps of .05sec. The changes in oscillatory power locked to the onset of the stimulus (i.e. word one) were calculated in regard to the change in power from baseline. The data were baseline corrected to -600 to -100ms prior to stimulus onset (i.e. presentation of first word).

To ensure that the observed oscillatory changes were not just the spectral representation of the ERPs, the ERP components were subtracted from the TFR (Mazaheri & Picton, 2005). The subtraction was achieved by first generating the time frequency decomposition of the ERP data for each condition and participant separately. Next, this time frequency power spectra (of the ERP) was subtracted from the time frequency power spectra of the EEG signal for each condition. The subsequent power changes in the time-frequency domain were used to generate time frequency power spectra differences between experimental conditions (lexical retrieval/semantic binding vs no lexical retrieval/ semantic binding; plausible semantic binding vs implausible semantic binding) for each group separately.

Finally, the statistical differences of the experimental condition differences in the power changes in the time-frequency domain were assessed by using a non-parametric cluster-based permutation test (using FieldTrip toolbox) (Maris & Oostenveld, 2007). Each channel/time/frequency pair locked to the onset of the first word for the difference between each experimental condition (i.e. binding vs no binding) was compared using an independent samples t-test (for young vs older adults) with a threshold at 5% significance level. Significant pairs were then clustered (cluster was defined based on proximity in space using the triangulation method i.e., having at least two significant electrodes that were adjacent to each other) and participants' labels of each cluster were randomly shuffled using 1000 partitions. The Monte Carlo P values were calculated using the highest sum of the test statistic. An equivalent dependent samples t-test was used to compare the experimental manipulations within each group separately in order to extract between condition effects. The time window used to assess the statistical differences in time-frequency power for (1) lexical and semantic binding manipulation was 0 (onset of word 1) to 3.2sec, where onset of word 2 occurred at 1.8sec, and (2) plausibility manipulation was 1.8sec (onset of word 2) to 3.2sec. The above analysis was performed within the following pre-defined frequency bands: theta (4-7Hz), alpha (8-14Hz), low beta (15-20Hz), and high beta (20-25Hz) consistent with previous studies (Poulisse et al., 2020; Segaert, et al., 2018).

Results

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We first visually inspected the TFRs and qualitatively describe the power modulations. The onset of word 1 and word 2 generated an increase in theta (4-7Hz) power, followed by a suppression of alpha power (8-14Hz), irrespective of condition in both age groups (Figure 3). Consistent with previous studies (e.g., Bastiaansen et al., 2005, 2008; Hermes et al., 2014; Mazaheri, et al., 2018), the theta power increase peaked at around 0.2 sec post word onset and was maximal over the occipital channels. Also in line with previous work, the alpha power suppression peaked at around 0.5sec post word onset and was maximal over the occipital channels (Davidson & Indefrey, 2007; Mazaheri, et al., 2018).

Our analysis approach was as follows. We focused our analysis on the oscillatory changes in the EEG associated with lexical processing (e.g., 1st word: swift vs. swrfeq) and semantic binding (e.g., horse when preceded by swift vs. when preceded by swrfeq). To help with the interpretation of the between-group effects, in the main text we only describe the significant oscillatory differences between conditions within groups (Figure 3A and B) *if* they were also significantly different between young and older adults (Figure 3C). A comprehensive and more detailed description of condition differences within each age group separately can be found in the supplementary materials (and Suppl. Figure 1).

In what follows, we first describe the lexical retrieval results, and then the semantic binding results.

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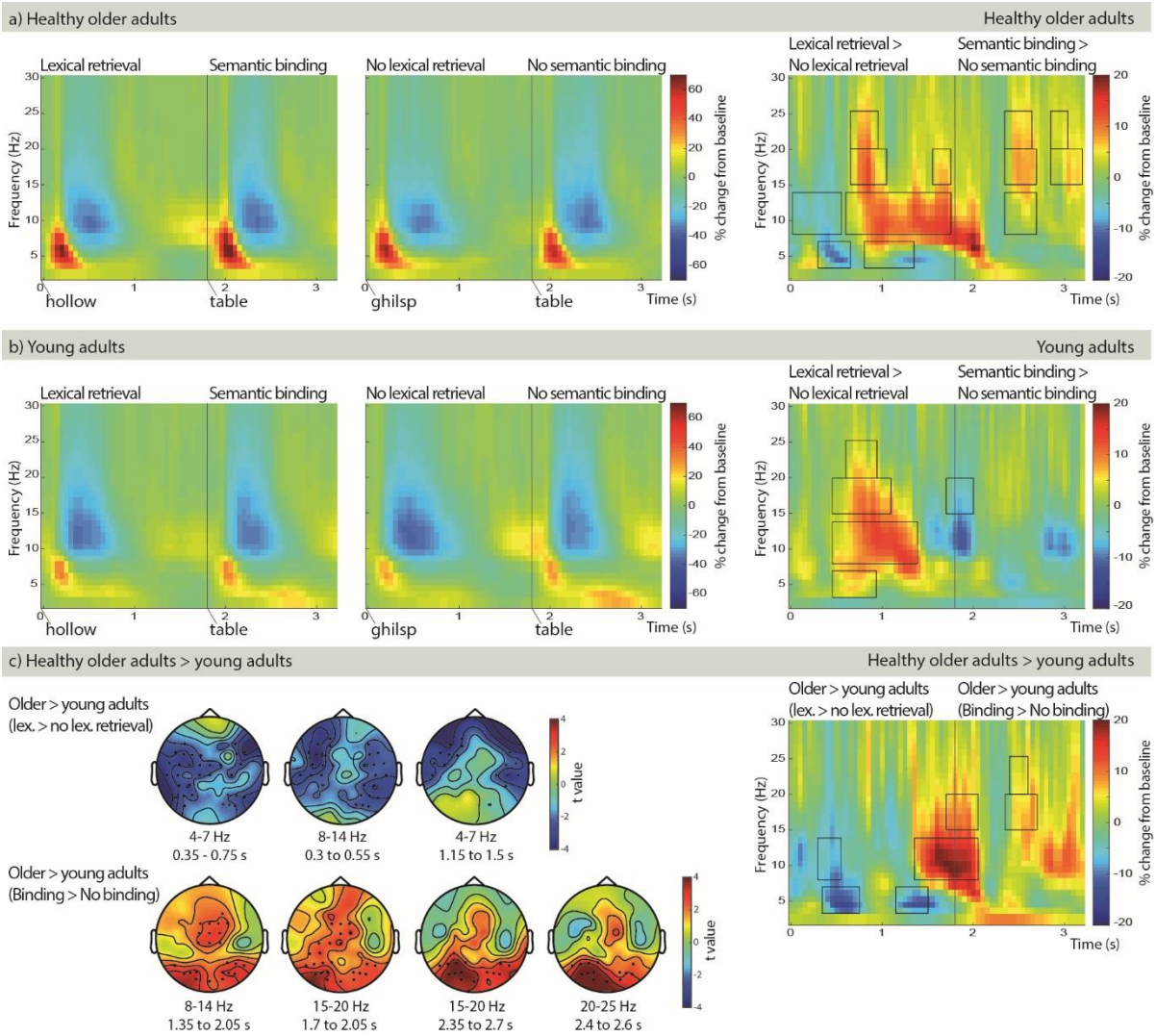

Figure 3. TFRs of power (collapsed across all electrodes) for lexical retrieval/semantic binding and no lexical retrieval/no binding, in (A) the healthy older adults, and (B) the young adults. (C) The condition differences in older adults minus the condition differences in young adults. Head plots are illustrating the clusters of electrodes that show the most pronounced mean condition difference for the healthy older adults vs. the young adults. Squares indicate significant group differences ($p<0.05$, cluster corrected).

Lexical retrieval results

We investigated lexical retrieval effects through comparison of power differences in the word 1 time window, comparing real words (i.e. lexical retrieval) to letter strings (i.e. no lexical retrieval can successfully take place (e.g., swift vs. swrfeq)). We observed significant differences between age groups for the lexical retrieval effects, in the theta (4-7Hz) and alpha (8-14Hz) range (Figure 3C). We discuss these in turn below.

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Theta power modulations for lexical processing show opposing patterns for healthy older adults and young adults

We observed significant differences between the age groups for lexical retrieval (i.e. lexical retrieval minus no lexical retrieval), in EEG activity in the theta (4-7Hz). Specifically, theta was attenuated 0.35 to 0.75sec after the first word during lexical retrieval in the healthy older participant group relative to the young adult group ($p<.008$).This difference in theta activity between the age groups was maximal over occipito-temporal electrodes. The age-group difference in theta activity during lexical retrieval emerged due to opposing patterns of theta modulation in relation to lexical and no lexical processing trials. Specifically, within the healthy older adults there was a smaller increase in theta power (0.3 to 0.65sec, $p = .005$) for lexical compared to no lexical retrieval, maximal over right occipital and left central electrodes (Figure 3A). However, in contrast the young adults showed a greater increase in theta power for lexical compared to no lexical retrieval in a similar time window (0.45 to 0.95sec, $p = .017$), maximal over left occipital and parietal electrodes (Figure 3B).

In addition, we observed differences in theta power related to lexical processing in a later time window, i.e. 1.15 to 1.50sec ($p = .022$) with the power being attenuated in the elderly group compared to the young participants. This age-group difference emerged due to an increase in theta activity in the non-lexical relative to the lexical condition (0.8 to 1.35sec, $p <.001$) in the elderly participants, which was absent in the young group.

An early and late post-word alpha modulation is present for lexical processing in healthy older but not young adults.

We observed a significant group difference in the modulation of alpha power (8-14Hz) in the 0.3 to 0.55sec time window ($p = .039$), over the temporal electrodes. This group difference emerged as a result of a greater post-word alpha suppression in the lexical retrieval compared to the no lexical retrieval condition in the healthy older adults (0 to 0.55sec, $p = .017$), which was not present in the young adults.

We also observed a significant group difference in the alpha modulation (8-14Hz) much later after the onset of the first word (1.35 to 2.05sec = .029) which was maximal over occipital and central electrodes. This group difference emerged due to an opposite pattern of alpha power rebound during lexical processing between the older and young adults. In the older adults the alpha power rebound following the post-word alpha suppression was greater in the lexical retrieval trials than the no lexical retrieval trials (from 0.6 to 1.75sec, $p < .001$). On the

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other hand a reversed pattern was seen in the young participant group with the alpha rebound being greater in the no-lexical retrieval trials compared to the lexical retrieval trials (1.7 to 2sec, p = .089). We interpret the attenuated alpha rebound to reflect an absence of closure in the no lexical retrieval condition in the older adults. Specifically, we hypothesize that the older adults continue to try and retrieve a lexical item (for a longer time than the young adults) after the onset of a pseudo word. Finally, it must be noted that the alpha rebound overlaps with the onset of the second word (word to be semantically integrated). It is possible therefore that the between-group difference in alpha rebound must be partly attributed to semantic binding (discussed further below) rather than exclusively lexical processes.

Lexical retrieval results summary

Summarizing above significant between-group differences in lexical retrieval, we find that the older and young adults appear to exhibit opposite patterns of theta and alpha modulation after the onset of real words (i.e. lexical retrieval) vs letter strings (i.e. no successful lexical retrieval).

Semantic binding results

Semantic binding effects were defined by comparing oscillatory power surrounding the onset of a second (i.e. target) word in a semantic binding to a no semantic binding context (e.g., *horse* when preceded by *swift* vs. when preceded by *swrfeq*). We observed significant differences between age groups for the semantic binding effects, in the alpha (8-14Hz), low beta (15-20Hz) and high beta range (20-25Hz) (Figure 3C). We discuss these in turn below.

Alpha and beta power in a time window that starts preceding the onset of the target word was differentially modulated across the age groups

First, as mentioned above there was a significant between-group difference in the alpha band (8-14Hz) in the 1.35 to 2.05sec time window (p = .029) over occipital and central electrodes. Although within-groups there were no significant condition differences, for young adults we observed that the alpha rebound was attenuated preceding and after the target word in the semantic binding condition compared to the no semantic binding condition. On the other hand for older adults in the equivalent time window an opposite pattern was observed with the alpha rebound being larger in the semantic binding relative to the no- semantic binding trials. The pattern just described in the alpha range, extends into the lower beta range (15-

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20Hz). There was a significant between-group effect in the time window of 1.7 to 2.05sec (p = .025), maximal over occipital, parietal and central electrodes. For young adults, there was a smaller low-beta increase from 1.7 to 2sec (p = .017) in the semantic binding compared to the no semantic binding condition, which was absent for older adults.

A later beta rebound was observed for semantic binding for the healthy older adults but not for the young group.

In addition, there were between-group effects in the lower beta (15-20Hz) and higher beta (25-30Hz) range over occipital electrodes in a slightly later timewindow, respectively 2.35 to 2.7sec (p = .008) and 2.4 to 2.6sec (p = .017). The between-group effect in the lower-beta and higher-beta range is driven by the older adults showing a clear semantic binding signature in this timewindow (with the effect extending into the alpha range), with no effect for the young adults in the equivalent timewindow. The healthy older adults elicited greater and more sustained suppression of lower-beta (2.35 to 2.7sec, p < .001), and more higher-beta suppression (2.35 to 2.65sec, p =.002) in the no semantic binding condition compared to the semantic binding condition.

Semantic binding results summary

Summarizing above significant between-group differences in semantic binding, we see that young and healthy older adults clearly have different semantic binding signatures. In young adults, there is an attenuation of the alpha rebound in anticipation of the target word onset, followed by a binding signature in the low-beta band (i.e. a smaller low-beta increase in the semantic binding compared to the no semantic binding condition) immediately preceding and during the presentation of the target, to-be-integrated, word. In contrast, during the semantic binding condition the older adults exhibited a smaller decrease in high and low beta activity (compared to no semantic binding) starting only at 500ms after the onset of the target word, which was not present in the young adults.

No effects of plausibility

We carried out a non-parametric cluster-based permutation analysis within the 1.8 to 3.2sec timewindow of interest with pre-defined frequency bands (described above) to compare plausible semantic binding (e.g. swift horse) to implausible semantic binding (e.g. barking horse). We found no significant differences in the power changes in any of the pre-defined frequency bands between healthy older and young adults. Important is that we do not take this to suggest that there are no age-related differences between young and older adults in the

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effects of plausibility on semantic integration, but rather, that our experiment was potentially not suited to reveal them. We must note that within the older adults group, the condition comparison between plausible and implausible semantic binding elicited no power differences; within the young adults a power difference was significant only in a very narrow 2 to 2.15sec timewindow (15-20Hz, p = .028). It is likely therefore that our plausibility manipulation was not strong enough to elicit reliable condition differences, in either age-group, and therefore our experimental manipulation may not have been sensitive enough to investigate potential age-related changes in processing plausibility.

Discussion

The current study used a minimal two-word phrase paradigm to investigate the differences in oscillatory activity (in the theta, alpha, and beta range) during lexical retrieval and semantic binding in healthy older vs. young adults. Lexical retrieval was assessed by comparing neural patterns during the presentation of real words (e.g., swift) vs. letterstrings (e.g., swrfeq). Semantic binding was examined by comparing neural patterns between semantic binding (e.g., horse, preceded by swift) and no semantic binding (e.g., horse, preceded by swrfeq) conditions. With regards to lexical processing we found that the older and younger groups at times exhibited opposite patterns of theta and alpha modulation at specific time intervals after the onset of the words, which as a combined picture suggest that lexical retrieval is associated with different and delayed signatures in older compared to young adults. Interestingly, with respect to semantic binding, we observed a signature in the low-beta range for young adults (i.e. a smaller increase for semantic binding relative to no binding) surrounding the presentation of the target word, while the semantic binding signature for older adults occurred about ~500ms later as a smaller low- and high-beta decrease (for binding compared to no binding). We will now discuss each of these findings in more detail in relation to previous literature.

Age-related oscillatory patterns linked to lexical retrieval

Firstly, we found that the oscillatory patterns observed during lexical retrieval (i.e. post word one onset) were different for healthy older adults compared to young adults. The presentation of word one (regardless of condition) led to an increase in theta power across both age groups, which has previously been proposed to be linked with the role of long-term memory retrieval (Bastiaansen et al., 2002, 2008; Bastiaansen & Hagoort, 2006). The lexical retrieval

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effect (i.e. real word vs letterstring) was associated with a greater theta increase closely followed after the first word onset (0.45 to 0.95sec) in young adults over the left temporal and parietal sites, suggesting greater demand on retrieving the meaning of 'real' words from long term memory. In other words, the effort required to retrieve an item containing lexical information was greater compared to when the item lacked lexical representation. This is consistent with previous studies (Bastiaansen et al., 2005; Marinkovic et al., 2012; Mellem et al., 2013; Weiss et al., 2005) who found that items that carry greater meaning or are more complex (i.e. real words and open class words) elicit stronger theta response compared to items that lack (or have lesser) lexical representation (i.e. pseudo words and closed class words) in young adults. In contrast, amongst healthy older adults, the lexical retrieval effect was associated with a theta increase which was smaller closely after word one onset (0.3 to 0.65sec) and then bigger (0.8 to 1.35sec) in the lexical retrieval condition (vs. no lexical retrieval). In other words, the 'typical' lexical effect (i.e. greater theta increase in the lexical retrieval compared to no lexical retrieval condition) occurred ~350ms later in healthy older adults compared to young adults, suggesting that it takes longer for healthy older adults to retrieve a lexical item from memory. This is contrary to Mellem et al., (2012) who did not find any theta power differences associated with lexico-semantic processing when comparing open and closed class words in older adults (although the lexical manipulations differ between the current study and Mellem et al., (2012), both paradigms manipulated the level of lexical charge). Additionally, this theta power difference between lexical vs. no lexical retrieval was prominent over a more widely spread network in healthy older adults including the bilateral occipital and central electrodes compared to young adults where it was lateralised to the left temporal and parietal sites. This is in line with the frequently found tendency for healthy older adults to show a lesser engagement of task relevant regions but a greater involvement of other regions compared to young adults (Cabeza et al., 1997, 2002; Grady, 2000). Furthermore, the Hemispheric Asymmetry Reduction in older adults (HAROLD) model (Cabeza, 2002) suggested that the neural processing in healthy older adults is associated with a decrease in hemispheric asymmetry (whereas young adults show lateralization to one side), which is evident in the theta activity in the current study.

Furthermore, we observed that healthy older adults elicited a greater alpha suppression in the lexical retrieval condition compared to the no lexical retrieval condition immediately after the first word onset, lasting for ~550ms, a signature which young adults do not display. The alpha suppression effect in healthy older adults is in line with Mellem et al., (2012), who

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found that words involving more lexical-semantic retrieval (i.e. open class words/lexical retrieval condition) were associated with a greater alpha suppression compared to closed class words in older adults in a similar time window (~200-600ms) following the onset of the word on the screen. Our results support the notion that early alpha suppression may be associated with operations involving lexico-semantic retrieval in healthy older adults. Note that we also found smaller alpha suppression in the lexical retrieval compared to no lexical retrieval condition in a later time window (beginning at 0.6sec for healthy older adults and 0.45sec for young adults) across both of the groups. However, this effect did not significantly differ between healthy older and young adults. This is in line with previous literature and the view that lexical search takes less time and effort for real words (as they carry lexical meaning) compared to letterstrings and this is consistent across both groups (Heim et al., 2005, 2007). Finally, the older adults did not show an alpha rebound like the young adults: while young adults showed an alpha rebound that was greater in the no-lexical retrieval compared to the lexical retrieval, the older adults showed the opposite. We interpret this to reflect an absence of closure in the no lexical retrieval condition in the older adults: older adults may continue to try and retrieve a lexical item (for a longer time than the young adults) after the onset of a pseudo word. In other words, processing of the non-lexical item was not fully complete, consistent with a finding in previous ageing studies with a similar paradigm (Poulisse et al., 2020).

Age related oscillatory patterns linked to semantic binding

Most interestingly, we observed oscillatory differences between healthy older and young adults during and after word two onset. The target word in the semantic binding condition required participants to retrieve the lexico-semantic information from memory, and, to develop a complex meaning representation of the two-word phrase. The latter was absent in the no semantic binding condition where the combination of a letterstring and a real word cannot create a meaningful phrase. We observed clearly different semantic binding signatures (i.e. comparing the target words in the semantic binding vs. no semantic binding condition) for the young vs. healthy older adult groups. These are novel findings as few previous studies have investigated the effect of ageing on the oscillatory dynamics associated with semantic binding.

The semantic binding effect was associated with an oscillatory brain activity difference in the alpha (1.35 to 2.05sec) and low-beta (1.7 to 2sec) frequency bands between healthy older and

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young participants. The first part of the group difference in the alpha band (up until around 1.7sec) occurred due to older adults eliciting an atypical alpha rebound response in the no lexical retrieval condition, whereas the young adults had no condition effect in the same time window (already discussed above under the header "Age-related oscillatory patterns linked to lexical retrieval").

Young adults elicited a smaller low-beta increase in the semantic binding condition (vs. no semantic binding) in a time-window immediately preceding and during the presentation of the to-be-integrated target word (from 1.7 to 2sec for low-beta). This early binding signature in the young adults within the beta band is somewhat consistent with previous studies. Beta frequencies have previously been proposed to be "carriers" of linguistic information and are involved in binding past and present inputs (Weiss & Mueller, 2012). For example, von Stein et al., (1999) found coherence exclusively in the beta frequency range between left temporal and parietal sites during semantic binding across visual and auditory modalities. Additionally, Berghoff et al., (2005) showed that figurative compared to literal sentences elicited increased coherence in the beta band between the hemispheres during the binding of semantic related information. On the other hand, past literature found some contrary effects to our results regarding beta power change during semantic binding as well. Luo et al., (2010) showed that semantically incongruous sentences elicited a reduced beta power 0 to 200ms post presentation of the critical word (compared to congruous sentences). This is opposing to our findings as during this time window the young adults displayed a reduced beta power in the semantic binding condition (equivalent to the semantically congruous sentences) compared to the no binding condition (equivalent to the semantically incongruous sentences).

Compared to the young adults, the binding signature in the healthy older adult group was different, and moreover delayed by about 500ms. Healthy older adults elicited a smaller beta decrease in the semantic binding condition (vs. no semantic binding). This semantic binding effect in healthy older adults is consistent with Kielar et al., (2015) who found that the processing of semantically violated sentences (somewhat similar to our no semantic binding condition) was associated with a greater 8-30Hz power decrease ~500ms post item onset compared to when the sentence was semantically correct (semantic binding condition). Similarly, Meltzer et al., (2017) observed a greater magnitude of 8-30Hz event related desynchronization for word lists (no semantic binding condition) compared to sentences (semantic binding condition). However, both studies also observed this effect in young

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adults, and therefore it may be surprising we do not see this condition difference in the young group in an equivalent timewindow.

The binding signature we see for healthy older adults is not only delayed but also in the opposite direction to that of the young adults. The finding of an inverse effect between a young and older adult age group is similar to some previous studies. For example, Beese et al., (2019) in an auditory sentence comprehension study tested whether oscillatory power differed across age groups when comparing correctly and incorrectly encoded sentences. They reported that young adults displayed a negative effect (later remembered vs later not remembered sentences produced an alpha decrease). This effect was attenuated in the middle aged adults and completely inversed in older adults (later remembered vs later not remembered sentences produced an alpha increase). The authors attributed this alpha band effect to a shift from cortical disinhibition to inhibition during sentence encoding. Additionally, Poulisse et al., (2020) also found an inverse condition effect between older and young adults in a syntactic binding context (in a two-word phrase paradigm). However, this inverse effect was contrary to our findings (i.e. they found that the syntactic binding effect was associated with a larger alpha power increase in young adults, and a smaller alpha power increase amongst the older adults). Although this pattern is the opposite of our results, our paradigm manipulated semantic and not syntactic binding. Also, it is important to note that Poulisse et al., (2020) observed this inverse condition effect between the groups in a much later time window (0.6-1.05sec) after the phrase presentation compared to our study (0-0.3sec).

As changes in the beta frequencies echo the role of language-related binding (Weiss & Mueller, 2012), we summarize that the semantic binding signature (reflected in the beta frequency) occurred *during* the presentation of the target word (which is when the semantic binding process takes place) in the young adults and was delayed by ~500ms in the healthy older group.

Suggestions for future research

We found different neural signatures in oscillatory power for young vs. healthy older adults in the present study. Differing functional neural patterns in healthy older adults are commonly interpreted as being compensatory (e.g., Cabeza et al., 2002). However, the term compensation should be reserved for differing neural patterns which are contributing meaningfully to performance (Cabeza et al., 2018; Grady, 2012). The present study was not

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designed to relate changes in brain function to language performance. Ideally, future studies would incorporate a trial-by-trial semantic comprehension performance measure and characterize which changes in network dynamics are predictive of successful language performance. Investigating the direct relationship between age-related functional neural changes and behavioural performance would be a particularly interesting avenue for future research, and be a necessary step in answering the fundamental question of how the ageing brain adapts to structural decline and reorganises its mechanistic functioning to support language comprehension.

In the present study, we used an experimental paradigm that focused on semantic binding, while minimizing contributions of the ability to make predictions. However, natural language comprehension does rely to some extent on actively making predictions. Making predictions gives language processing a head start (Kuperberg & Jaeger, 2016). Previous studies on young adults have found an alpha power decrease prior to the onset of predictable words (Rommers et al., 2017; Wang et al., 2017), suggesting that in young adults anticipatory binding processes are initiated prior to predictable words being presented. A number of ERP studies have demonstrated that there are age-related changes in the ability to engage prediction mechanisms. Age-related changes in processing predictable sentence endings were evident by the lack of a frontal positivity effect for older (compared to young) adults (Wlotko et al., 2012). Also N400 amplitudes suggest that older adults do not use the sentence context to pre-activate semantic features of predictable words (Federmeier et al., 2002). Future studies could extend on these findings and examine the age-related changes in oscillatory dynamics supporting the use of predictions during semantic binding.

Lastly, future research should incorporate individual differences measures (and thus, larger sample sizes) to assess which non-linguistic cognitive resources and brain structure properties support the implementation of age-related changes in functional neural characteristics (Peelle, 2019). A quantitative shift in capacity constraints (e.g. higher working memory) can qualitatively impact on the way language is processed, for example, making older adults more able to use contextual semantic information or predictions. Moreover, sufficiently flexible cognitive resources can work together to circumvent structural decline and support functional adaptations, maintaining successful language and communication performance.

Summary

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Healthy older adults have a different oscillatory signature for semantic binding compared to young adults: young adults elicit an early semantic binding signature, around the target word presentation, in the form of a smaller low-beta increase during semantic binding (compared to no semantic binding). On the other hand, healthy older adults display a semantic binding signature ~500ms later, with a smaller low/high-beta decrease in the semantic binding condition (compared to no semantic binding). Our findings are in line with previous literature that older adults do extract and make use of contextual semantic information, but there are differences (compared to young adults) with respect to when and how this happens (Federmeier et al., 2003; Federmeier & Kutas, 2005; Stine-Morrow et al., 1999; Wlotko & Federmeier, 2012).

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