Running Head: AGING & INVOLUNTARY MEMORY

Increased alpha suppression with age during involuntary memory retrieval

Henderson, S. E.[1], Hall, S. A.[2], Callegari, J. M.[1], Desjardins, J. A.[1], Segalowitz, S. J.[1], &

Campbell, K. L.[1]

[1]Department of Psychology, Brock University, Canada

[2]Department of Psychiatry and Behavioral Sciences, Duke University, USA

Address correspondence to:
Karen L. Campbell
Department of Psychology
Brock University
1812 Sir Isaac Brock Way
St. Catharines, ON L2S 3A1, Canada
karen.campbell@brocku.ca

Abstract

Recent work suggests that while voluntary episodic memory declines with age, involuntary episodic memory, which comes to mind spontaneously without intention, remains relatively intact. However, the neurophysiology underlying these differences has yet to be established. The current study used EEG to investigate voluntary and involuntary retrieval in older and younger adults. Participants first encoded sounds, half of which were paired with pictures, the other half unpaired. EEG was then recorded as they listened to the sounds, with participants in the involuntary group performing a sound localization cover task, and those in the voluntary group additionally attempting to recall the associated pictures. Participants later reported which sounds brought the paired picture to mind during the localization task. Reaction times on the localization task were slower for voluntary than involuntary retrieval and for paired than unpaired sounds, possibly reflecting increased attentional demands of voluntary retrieval and interference from reactivation of the associated pictures, respectively. For the EEG analyses, young adults showed greater alpha event-related desynchronization (ERD) during voluntary than involuntary retrieval at frontal and occipital sites, while older adults showed pronounced alpha ERD regardless of intention. Additionally, older adults showed greater ERD for paired than unpaired sounds at occipital sites, likely reflecting visual reactivation of the associated pictures. Young adults did not show this alpha ERD memory effect. Taken together, these data suggest that involuntary memory is largely preserved with age, but this may be due to older adults' greater recruitment of top-down control even when demand for such control is limited.

Keywords: memory, aging, oscillations, intentionality, cognitive control

1. Introduction

There is a prevailing view in the cognitive aging literature, and in society more broadly, that memory declines with age, particularly memory for events (or *episodic memory*; Craik & Byrd, 1982). However, aging research has, until very recently, focussed largely on the study of voluntary episodic memory, or memories for events that are intentionally brought to mind, while ignoring involuntary episodic memory, or memories for events that come to mind spontaneously without intention (Berntsen, 2010; Maillet & Schacter, 2016). These are distinct in that voluntary memory retrieval requires an active and intentional memory search, while involuntary memories are brought to mind without any effort, arising in response to internal or external cues, or in a seemingly random fashion (Berntsen, 1996). While these involuntary memories are unique in their apparent spontaneity, the nature of their mental representation may be quite similar to voluntarily remembered episodes (i.e., specific in time and place, rich in detail and emotion, brought into conscious awareness). Though involuntary memory is less frequently studied, it has long been recognized as an important aspect of our everyday experience and reflects one of Ebbinghaus' (1885) three main memory types, which we would now define as voluntary explicit, involuntary explicit, and implicit memory. Indeed, involuntary memories are central to our understanding of our conscious experience, as they arise as frequently as voluntary memories and may guide our actions in daily life (Rubin & Berntsen, 2009; Berntsen, 2010).

Recent work suggests that involuntary memory is preserved, at least in some capacities, with increasing age (Schlagman et al., 2009; Berntsen et al., 2015). Naturalistic investigations of involuntary memory using diary reports have found that the frequency of involuntary autobiographical memories in daily life does not decline with age (Berntsen et al., 2015). In contrast, older adults report voluntary memories more slowly and with less specificity compared

to younger adults (Schlagman et al., 2009). Older adults' preserved involuntary memory has also

been demonstrated in the lab, using a more controlled paradigm in which participants viewed the

same movie twice (with voluntary and involuntary memories assessed during the second

viewing; Berntsen et al., 2017). Older and younger adults reported a similar number of

involuntary memories when watching the film a second time, but older adults were slower and

recalled fewer voluntary memories. Collectively, this work suggests that involuntary memory is

preserved with age in both the lab and more naturalistic settings. However, the cognitive and

neural mechanisms underlying the differential effects of age on voluntary and involuntary

memory are still poorly understood.

1.1 Neural Underpinnings of Voluntary vs. Involuntary Memory

While the neural underpinnings of voluntary episodic memory have been studied

extensively, few imaging studies have looked at involuntary retrieval. Hall et al. (2014)

examined this question in young adults using experimentally encoded sound-picture pairs while

manipulating retrieval conditions via task instructions. Their work suggests that reactivation of a

visual memory (regardless of the intention to retrieve) is associated with increased activity in

regions typically involved in memory retrieval, including the medial temporal lobe, posterior

midline, ventral parietal cortex, and occipital regions. Voluntary memory was additionally

associated with increased activity in the dorsolateral prefrontal cortex (dlPFC), which suggests

that voluntary retrieval alone engages regions associated with top-down control.

A similar dissociation between the intention to retrieve and retrieval success itself was

also observed in a study combining EEG and fMRI (Kompus et al., 2011). In this study, memory

for environmental sounds and pictures of objects was associated with activation in the posterior

hippocampus and increased amplitude of the P600 (representing the left parietal old/new effect

in EEG) in a manner that was not modulated by the intention to retrieve (see also Curran, 1999).

In contrast, both imaging methods revealed effects of retrieval intentionality that were

independent of retrieval success, with greater right dorsolateral and left anterior prefrontal cortex

activation, and selective increases in parieto-occipital N1 amplitude for unintentionally retrieved

items. Thus, the intention to retrieve is uniquely associated with increased activity in top-down

control regions (see also Dobbins et al., 2003), while reactivation of the memory itself,

regardless of intention, is associated with activity in more posterior memory-related and

perceptual processing regions.

1.2 Memory Effects in EEG

Electroencephalography (EEG), with its high temporal resolution, may be the best

method for distinguishing between controlled and automatic processes at retrieval. One of the

most common ways to analyze EEG data is to examine event-related potentials (ERPs), that is,

averaged EEG signal time-locked to an event. ERP studies of memory and aging suggest that

there are dissociable effects of age on recollection (reflecting slower, more controlled retrieval)

and familiarity (reflecting more automatic processes). Older adults show reduced recollection-

related parietal old/new effects around 500-700 ms post stimulus (Friedman et al., 2010), but

relatively preserved mid-frontal familiarity effects around 300-500 ms (Nessler et al., 2007;

Friedman et al., 2010). Since recollection is thought to be more dependent on effortful control

than is familiarity (Jacoby, 1991; Jennings & Jacoby, 1993), we might expect a similar pattern of

results when contrasting voluntary vs involuntary retrieval. Indeed, recent work suggests that

unintentional recognition (of distractors) is associated with the rapid and automatic familiarity

process, while intentional recognition additionally employs a slower and voluntarily controlled

recollection process (Bergström et al., 2016), and age has a greater impact on the latter (Allen et

al., 2020). However, ERP findings are mixed, with older adults sometimes showing preserved

recollection (Friedman et al., 2010; James et al., 2016) and reduced familiarity effects (Duarte et

al., 2006; Wang et al., 2012), possibly due to increased between-subject variability with age

(reviewed by Friedman, 2013). These inconsistencies may also be partially attributable to age-

related increases in within-subject temporal variability of ERPs (Murray et al., 2019). Thus,

despite the utility of ERPs in providing precise temporal resolution, the integration of

complementary analysis methods is critical in developing a more robust understanding of age

differences in brain function.

Another way to examine the neural correlates of memory is through event-related

synchronization (ERS) and desynchronization (ERD) within specific frequency bands of the

EEG signal (Hanslmayr et al., 2016). In particular, alpha (8-12 Hz) and beta (13-30 Hz) ERD

have been positively associated with the encoding and reactivation of memories (Klimesch et al.,

1996; Burgess & Gruzelier, 2000; Hanslmayr et al., 2012; Waldhauser et al., 2016), and track the

fidelity of stimulus-specific cortical representations (Griffiths et al., 2019). This relationship

between alpha and beta ERD and memory is thought to reflect the richness or detail of mental

representations via increased neocortical firing rates (Hanslmayr et al., 2012). Accordingly, alpha

ERD has been shown to vary systematically with the number of items retrieved as well as

showing differences in topography according to the modality of the remembered stimuli

(Burgess & Gruzelier, 2000; Khader & Rösler, 2011). Alpha and beta ERD have also been

associated with the reactivation of visual information at retrieval, with greater ERD at occipital

sites contralateral to the visual field at encoding (Waldhauser et al., 2012). Although we are

unaware of any studies using ERD to investigate involuntary memory, previous work suggests

that voluntary and involuntary memory share similar patterns of neural activation in posterior

perceptual regions (Hall et al., 2014). Thus, one might expect similar patterns of oscillatory activity at occipital sites for both voluntary and involuntary retrieval.

Few studies have examined age differences in memory-related alpha activity to date. However, there is some evidence that older adults show similar memory-related oscillatory activity during intentional retrieval from both long-term (Allen et al., 2020) and short-term memory (Karrasch et al., 2004), albeit with less alpha ERD in older adults (Karrasch et al., 2004). Additionally, subsequent memory effects reflected by increased alpha ERD have been observed in both older and younger adults and have been shown to relate to memory performance in a non-age-dependent manner (Strunk & Duarte, 2019).

In addition to these oscillation-based memory effects, alpha ERD has also been linked more generally to cortical activation (Klimesch et al., 2007; Klimesch, 2012). Alpha ERD at frontal sites is thought to reflect activation of frontal control processes, including executive control, directed attention, and effortful cognitive reappraisal (Klimesch, 2012; Misselhorn et al., 2019; Tschentscher & Hauk, 2016; Parvaz et al., 2012). At occipital sites, alpha ERD has been associated with attention using visual stimuli (Pfurtscheller et al., 1994), as well as in a modality-independent manner (Peng et al., 2015). Widespread alpha ERD, particularly in the lower alpha band (8-10 Hz), has further been associated with general attention facilitating cognitive tasks (Klimesch et al., 1999). Thus, we might expect alpha ERD over occipital sites to also track with attentional demands at retrieval.

1.3 Current Study

The goal of the current study is to characterize neural activity associated with voluntary and involuntary retrieval in younger and older adults. To accomplish this, we used a two-part paradigm adapted from Hall et al. (2014). In the first session, participants encoded a series of

semantically related sound-picture pairs and a series of unpaired sounds. To preserve the

involuntary retrieval manipulation, participants were told that this was a study investigating age

differences in the effect of context on sound localization.

In the second session, participants were randomly assigned to either the voluntary or

involuntary retrieval condition. EEG was recorded while sounds from the encoding phase were

replayed and participants had to decide whether the sound was louder on the left or right.

Participants in the voluntary condition were additionally instructed to retrieve the picture

associated with each sound. Reaction times (RTs) to the sounds were analyzed with the

expectation that RTs would be slower for paired than unpaired trials, reflecting interference from

retrieval of the associated images (Craik et al., 1996; Lozito & Mulligan, 2010). We also

expected RTs to be slower in the voluntary than involuntary retrieval condition, reflecting

interference from the intention to retrieve (Craik et al., 1996; Anderson et al., 1998; Fernandes &

Moscovitch, 2003). Thus, RTs on the localization task were used as an implicit measure of

memory reactivation and voluntariness of retrieval, and we expected this implicit measure to be

similar across the two age groups.

After the localization task, participants listened to the sounds again and retrospectively

reported for which sounds (during the sound localization task) they had remembered the

associated picture. We did not ask about memory during the localization task itself as this would

have alerted the involuntary group to the true nature of the task. We expected no age difference

in the number of retrospectively reported memories in the involuntary retrieval condition, given

previous work showing that involuntary memory is relatively preserved with age (Schlagman et

al., 2009; Berntsen et al., 2015; Berntsen et al., 2017). However, given previous demonstrations

of age-related declines in metacognition (Palmer et al., 2014; Hertzog & Curley, 2018) and the

retrospective nature of these reports, it is possible that age differences may emerge on these retrospective memory reports even in the involuntary condition.

In regards to the EEG data, we examined age differences in alpha ERD during the sound localization task within frontal and occipital ROIs designed to capture activity related to the intention to retrieve (by contrasting voluntary and involuntary retrieval) and visual reactivation of the associated picture (by contrasting paired and unpaired sounds). ERD may be particularly suited for the type of naturalistic stimuli used here (i.e., environmental sounds), as identification of these sounds may be protracted in time and poorly synchronized across participants. We expected greater frontal and occipital alpha ERD for voluntary than involuntary retrieval across both age groups, reflecting increased effortful control (Parvaz et al., 2012; Misselhorn et al., 2019) and external attention (Klimesch, 2012) associated with intentional retrieval. Further, we expected voluntariness to interact with age such that older adults may show greater frontal alpha ERD than younger adults in the involuntary condition, possibly reflecting frontal overactivation at lower levels of demand (e.g., Cappell et al., 2010; Grady, 2012). In contrast, younger adults were expected to show less frontal alpha ERD for involuntary than voluntary retrieval, in line with previous work showing decreased frontal activity during involuntary retrieval (Hall et al., 2014). Finally, we expected visual reactivation of memories to be reflected by greater alpha ERD for paired than unpaired sounds (particularly over occipital sites), reflecting reactivation of the picture associated with the paired sounds (Waldhauser et al., 2012). This difference in posterior alpha desynchrony should be similar for both voluntary and involuntary retrieval, which share a common episodic memory system (Hall et al., 2014; Niziurski & Berntsen, 2019).

2. Methods

2.1 Participants

Participants were 31 young adults (18-30 years; M = 21.06, SD = 2.83; 4 males) of which 15 were in the voluntary retrieval condition, and 35 older adults (65-80 years, M = 71.71, SD = 4.91; 10 males) of which 18 were in the voluntary retrieval condition. Our sample size was based on previous studies contrasting voluntary and involuntary retrieval (Hall et al., 2014) and memory effects on neural oscillations (Khader & Rösler, 2011). Two additional young and 2 additional older adults were recruited but failed to complete both sessions and are therefore excluded from analysis. Young adults were recruited from Brock University and received partial course credit for their participation. Older adults were recruited from the community and received monetary compensation of $10 per hour for their participation. All participants were right-handed and had normal or corrected to normal vision and hearing, and no history of neurological conditions which may influence the interpretation of electrophysiological recordings. Hearing was evaluated using a 12-item Hearing Screening Inventory (Coren and Hakstian, 1992), which has been shown to correlate highly with audiometric measures. The Montreal Cognitive Assessment (MOCA) (Nasreddine et al., 2005) was used to screen for mild cognitive impairment (see Table 1), and the Shipley vocabulary test was used to evaluate vocabulary knowledge (see Table 1).

Table 1.

Demographics, Hearing, and Cognitive Assessments.

	Young Adults				Older Adults				*Young vs Old (t)*
	Overall (M(SD)) n=31	Voluntary (M(SD)) n=15	Involuntary (M(SD)) n=16	*t*	Overall (M(SD)) n=35	Voluntary (M(SD)) n=18	Involuntary (M(SD)) n=17	*t*	
Age	21.1 (2.83)	21.1(3.31)	21.0(2.39)	0.09	71.7(4.91)	72.3(4.74)	71.1(5.17)	0.83	49.9**
Years of Education	14.7(1.42)	14.7(1.16)	14.6(1.70)	0.11	16.0(1.56)	16.7(4.94)	15.1(3.04)	1.50	1.57
Hearing	20.6(3.93)	20.2(3.91)	20.9(4.04)	0.44	23.0(5.15)	22.9(4.18)	23.1(6.16)	.072	2.10*
MOCA	27.4(1.91)	27.6(1.96)	27.2(1.91)	0.54	25.5(2.47)	26.5(1.92)	24.5(2.62)	2.74*	3.58**
Shipley	28.8(4.24)	28.6(3.33)	29.1(5.05)	0.34	34.7(3.19)	35.0(2.95)	34.4(3.48)	0.51	6.29**

*p<.05, **p<.001

2.2 Stimuli

Stimuli included 100 environmental sounds (e.g., dog panting, schoolyard sounds) and 100 semantically related pictures (e.g., golden retriever on a beach, kids playing in a schoolyard) adapted from those used by Hall and colleagues (2014; see Figure 1). The images were obtained from online image searches with the goal of obtaining neutral or positively valanced images that would not elicit a strong emotional response (stimuli uploaded to OSF, link available upon request). The sounds were obtained from the SUN database (http://groups.csail.mit.edu/vision/SUN/). The paired sounds and images were divided into two lists of 50 and counterbalanced across the paired/unpaired and voluntary/involuntary conditions. The paired sounds and images were designed such that they were related to but could not be

adequately described by simply describing the sound (e.g., panting sound with image of dog

lying on a beach). The sounds were calibrated to be equal volume and have a duration of 700ms.

During retrieval, the sounds were panned 50% to the left or right, such that the sounds were 50%

louder on one side to facilitate the sound localization cover task.

2.3 Electroencephalography (EEG)

EEG was recorded with a 128-channel Active Two BioSemi system with CMS/DRL

referencing. The sampling rate of the signals was 512 Hz which were digitized with a 24-bit

analogue to digital converter. The recordings were made in a dimly lit, electrically shielded room

and the visual stimuli were presented 60 cm from the participant. The auditory stimuli were

presented through ER-2 headphones with 30 dB external noise exclusion and 70 dB isolation

between ears. The volume was individually adjusted to a comfortable level using a calibration

sound unrelated to the stimuli.

2.4 Procedure

2.4.1 Overview

Participants performed a two-part experiment with an encoding procedure on the first

day, followed by a two-day break, after which participants returned for a recall session during

which EEG was recorded. A cover story was used to preserve the involuntary retrieval

manipulation, which stated that the study was investigating the effect of contextual images on a

sound localization task.

2.4.2 Session 1

Participants encoded 50 semantically related sound and picture pairs and 50 unpaired

sounds in a procedure adapted from Hall and colleagues (2014). Our aim was for participants to

learn these pairs so well that when the sound was played alone at retrieval, the picture would

come to mind automatically. Participants encoded the 50 paired stimuli three times: (i) the sound and picture were displayed simultaneously (with the same onset time), the sound for 700 ms while the picture remained on screen for 4 s, and the participant verbally produced a sentence integrating the paired items, which was typed by the researcher; (ii) each sound-picture pair was presented again followed by the participant's previously generated sentence, which the participant was given the opportunity to edit; (iii) the sound was presented on its own followed by a 2 s break during which the participant could imagine the picture that was paired with it, immediately followed by the presentation of the pair together with a final opportunity to edit their sentence (Figure 1A). The sound-picture pairs were encoded in three sequential blocks (with each pair appearing once in each block), followed by a block of encoding the unpaired sounds. The unpaired sounds were encoded by rating their uniqueness on an 8-point scale in comparison to the already encoded sounds (Figure 1B). The unpaired sounds were also 700 ms in length, followed by a 4 s response window. The sounds and pictures were counterbalanced such that each sound was in the paired category for half of the participants and in the unpaired category for the other half.

2.4.3 Session 2

Two days later, following EEG setup, the second session began with a re-encoding task for both the paired and unpaired sounds (Figure 1C). During the re-encoding run for the paired sounds, the sound (700 ms) and picture (4 s) were again presented simultaneously and participants were asked to consider the sentence they had previously generated (not represented this time) and rate on an 8-point scale how well the sound and picture went together given that sentence. The re-encoding of unpaired sounds was the same encoding task used in the first session, wherein participants were asked to rate the uniqueness of the sound on an 8-point scale.

The sound localization/recall task was then performed, in which the 50 paired and 50

unpaired sounds were randomly mixed and panned 50 % to the left or the right (Figure 1D).

Participants in the involuntary condition were asked to press with their index finger on the key

that corresponded to the side from which the sound was louder through their headphones. A

fixation cross was presented for a jittered amount of time between 500ms and 750ms before the

sound onset. Each sound was presented for 700ms and participants were instructed to wait until

after the sound and fixation cross (which persisted for 1000 ms) had offset before making their

response. Participants in the involuntary group were instructed not to actively attempt to bring

the pictures to mind but instructed that it was fine if the pictures came to mind spontaneously.

This was in accordance with Hall and colleagues (2014) who (in pilot testing) found that ratings

of effort during recall were lower in the involuntary group when explicitly instructed not to

actively attempt to bring pictures to mind, but also prevented participants from actively

suppressing retrieval. Participants in the voluntary group were presented with the same sound

localization task but were additionally asked to recall the pictures that had originally been paired

with the sounds in as much detail as possible while performing the localization task. All sounds

were played twice to maximize the number of trials for EEG analyses (200 trials in total, broken

up into blocks of 50 trials).

Following the sound localization task, participants completed two tasks to assess their

memory for the sound-picture pairs and to determine for which trials (during the sound

localization task) they had picture memories come to mind. In the first of these tasks, participants

were presented with both the paired and unpaired sounds intermixed and were asked to report

whether one of the previously learned pictures had come to mind when they heard the sound in

the previous localization task (yes/no). Since we did not think that participants would be able to

distinguish between the first and second sound localization blocks, they were not asked to report

in which block the image had come to mind. They were additionally asked to report the

vividness with which the picture had come to mind on an 8-point scale (0 = no picture, 7 = very

clear), as well as whether they had put effort into recalling the picture (yes/no), and finally, how

much effort they used on an 8-point scale (0 = no effort was made to remember, 7 = I tried quite

hard to remember) (Figure 1E). The subjective vividness and effort ratings were not further

analysed because there was little variability in these ratings and participants seemed to use them

as a marker of memory (i.e., giving high ratings when they said they remembered the picture and

low ratings when they did not). Finally, we measured explicit memory for the pairs in a final

cued recall task. The 50 sounds that had been originally paired with pictures were replayed again

and participants were asked to recall the associated picture in as much detail as possible. We

expected older adults to recall fewer pictures on this task given previous demonstrations of

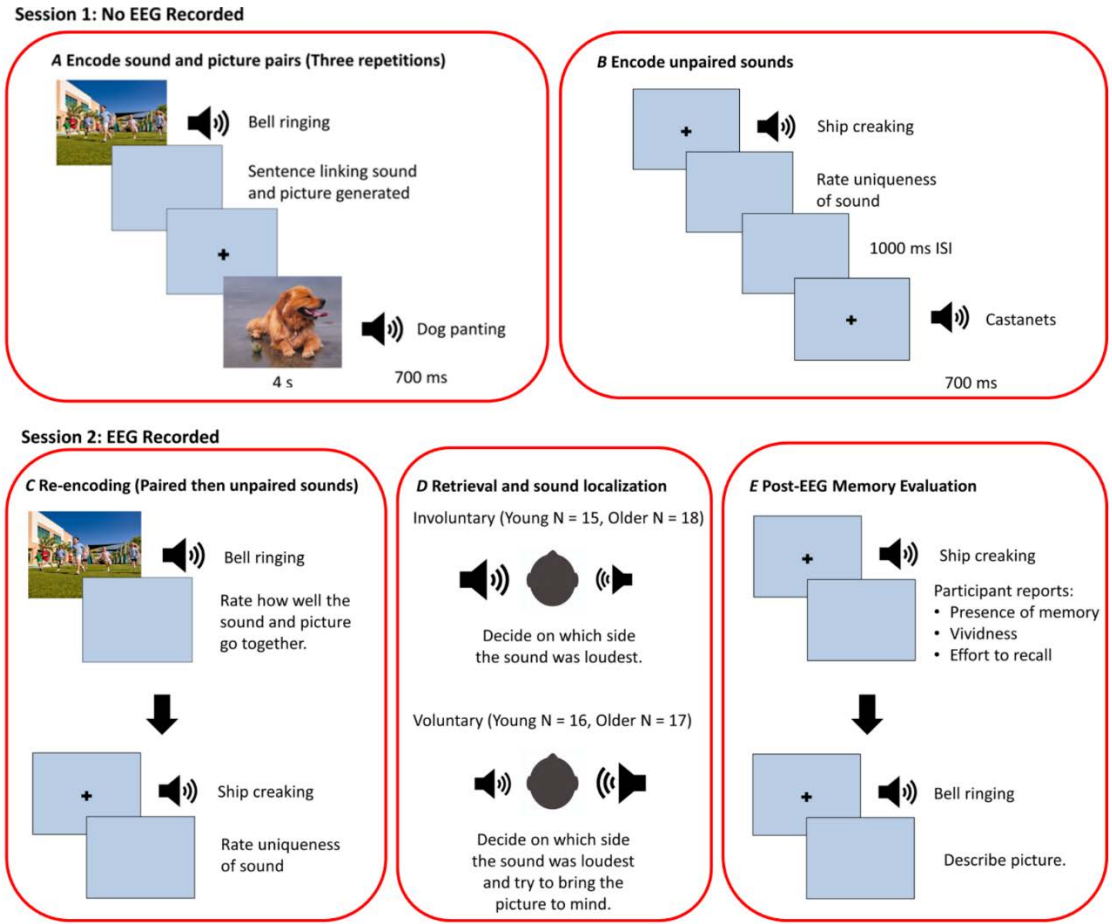reduced explicit associative memory with age (e.g., Old & Naveh-Benjamin, 2008).

Figure 1. Experimental protocol for Session 1 (in which pairs were encoded) and Session 2 (in which retrieval was evaluated using EEG). A. Participants encoded paired naturalistic sounds and images by forming sentences to link them. B. Participants heard the unpaired sounds and judged them on their uniqueness. A two-day break preceded Session 2. C. Participants re-encoded the paired sounds and images learned in Session 1 by rating how well they went together given the sentence they had generated previously. D. Participants were randomly assigned to voluntary or involuntary retrieval conditions. Both groups performed the sound localization cover task where they were asked to judge from which side the sounds were louder. The voluntary retrieval group was additionally asked to try to bring the paired images to mind. E. Participants heard all the sounds again and were asked to report which ones they had had memories for during the sound localization. Finally, they performed an explicit cued recall task to determine which pairs they could accurately remember.

2.5 Data Analysis Behavioural

2.5.1 Sound Localization Data

Percent accuracy for the sound localization task was calculated for each condition as the number of sounds correctly attributed to the correct source (left or right side) divided by the total number of sounds. Reaction times (RT) for correct responses on the sound localization cover task were also analysed. RTs were trimmed to retain those trials within 2.5 SD of the mean (within each individual/condition), and then averaged for each individual/condition. The analysis was limited to those participants who retained at least half of the trials (young adult n = 26, older adult n = 23) to facilitate the within-subjects comparison of trial types.

2.5.2 Memory Data

Memory performance was scored according to responses during the retrospective memory task and the final cued recall task. First, using the responses from the retrospective memory task, separate analyses were run for "yes" responses to paired sounds and unpaired sounds. These data could not be combined into a single ANOVA because "yes" responses to paired sounds is similar to correct responses on a cued recall task, while "yes" responses to unpaired sounds is similar to false alarms (in that these sounds were never paired with an image and thus, should not have resulted in a visual memory). Using the responses obtained from the final cued recall task, correctly remembered pairs were identified. A single rater who was blind to group and condition determined correctly recalled trials with the criteria that the descriptions contained sufficient detail to determine the picture being described and did not simply describe the sound alone (e.g., for the sound of children laughing, a correct response would be "a child hanging upside down on climber" rather than simply "a child").

2.6 Data Analysis EEG

2.6.1 Preprocessing

EEG data were pre-processed through an automated pipeline using custom code created

using MATlab 2012 and executed on the Compute Canada network. The automated

preprocessing procedure followed the steps described by Desjardins and Segalowitz (2013), and

van Noordt et al. (2015), which are described in detail in a recent methodological paper by

Desjardins et al. (2021). In short, this involved flagging channels and in-task time based on the

distribution of channel-neighbour correlations. This allowed the pipeline to identify and remove

artifacts to improve blind source separation using independent components analysis (ICA).

Cortical classifications of independent components were performed to remove non-cortical

components such as biological artifacts (e.g. eye blinks, muscle activity) and stationary noise.

Following the automated pre-processing steps, a quality control review was performed by a

single trained research assistant to confirm that decisions about the component classifications

were appropriately made during pre-processing. Time frequency decomposition was

accomplished with FFT using Hanning windows as tapers with a window length of 4000 ms that

slid over the data in 50 ms increments. The analysis was performed with 1 Hz steps from 3-30

Hz between -1500 and 3000 ms around the sound stimulus onset at retrieval. Power changes

were calculated in relation to a baseline window that spanned from -1000 to -500 ms pre-

stimulus onset to avoid eliminating important group differences (age group or voluntariness

condition) that may have arisen after fixation cross onset at -500 ms (e.g., age differences in

readiness or anticipatory attention; e.g., Morcom & Rugg, 2004; Capotosto et al., 2009).

2.6.2 Time Frequency Analysis

Given our a priori hypotheses that differences should arise at frontal and occipital sites,

we selected two groups of electrodes to represent these regions of interest (ROIs) to allow for

stronger claims to be made about the location of the effects than may otherwise be reasonable for the cluster-based statistical analysis we also employed (see below; Pernet et al., 2015). The frontal ROI was defined as the average across seven midfrontal electrodes (see Figure 3). The occipital ROI was defined as the average across eight occipital electrodes (see Figure 3). Within these ROIs, we examined age and condition differences across a range of frequencies (3-30 Hz). For each ROI, we performed two main analyses: 1) we compared voluntary with involuntary retrieval (for paired sounds only) to examine the effects of age and retrieval intention on alpha ERD and 2) we compared paired and unpaired sounds to determine if alpha ERD is more pronounced (particularly over occipital sites) for paired sounds, presumably reflecting visual reactivation of the associated picture. We used paired trials only for the voluntariness analysis to avoid introducing any additional variance which may not be attributable to voluntariness alone (e.g., thinking about how the unpaired sounds were never paired in the first place, particularly in the voluntary condition where participants were intentionally trying to remember a picture).

In addition to the ROI analysis, we also ran confirmatory whole scalp analyses using individual alpha frequency (IAF). Previous work has consistently shown age-related slowing in IAF (Woodruff & Kramer, 1979, Knyazeva et al., 2018). IAF has been shown to represent a stable individual trait (Grandy et al., 2013) and its use in research within and beyond the aging literature has become increasingly common. Since our aim in the present study was to establish age-related differences in oscillatory power, especially in the alpha frequency range, it was important to consider individual differences in IAF instead of taking the more traditional approach of averaging across a predefined alpha range. We computed IAF for each individual by plotting the mean power spectrum with 0.5 Hz precision over the whole scalp and visually inspecting spectra to detect peaks between 7 and 13 Hz. This yielded an average IAF of 11.10 Hz

(SD = 1.22) for younger adults, which was significantly higher than that of older adults, M =

10.37 Hz (SD = 1.14), $t = 2.50$, $p = .015$. Thus, to ensure that any observed age differences were

not artificially inflated by differences in peak IAF, whole scalp cluster analyses were run for all

age comparisons using the individualized frequency range which was averaged across IAF +/-2

Hz for each participant. These confirmatory analyses are presented in the Supplementary

Materials.

Trials were segmented according to paired and unpaired status as well as according to

retroactive memory performance. Subsequent analyses used all paired and unpaired sounds

rather than paired sounds that participants said they remembered and were correctly recalled on

the final cued recall test because older adults had fewer correctly remembered trials than younger

adults (making group comparisons difficult; see Table 2). Additionally, older and younger adults

may differ in their metacognitive abilities (Palmer et al., 2014); thus, using all paired sounds for

the memory analysis would reduce the likelihood of introducing error related to inaccurate

retrospective reporting of memory retrieval. This choice was further validated by comparing

older adults' neural activity during the sound localization task for all paired trials to only those

that they later reported as remembered and were able to correctly recall on the final cued recall

task (this analysis would not be very informative in the younger group given the small number of

forgotten trials). This comparison yielded no significant differences (ps >= .169). In a second

confirmatory analysis, we compared sounds that older participants said they had a memory for

with all unpaired trials. This yielded a similar pattern of results to the analysis using all paired

trials and thus, we report the analysis using all paired trials as it allowed for more even trial

numbers across age groups.

Statistical analyses of the EEG data were performed using FieldTrip software
(Oostenveld et al., 2011). To test for statistical differences between conditions we employed non-
parametric permutation tests with 1000 iterations and cluster-based correction for multiple
comparisons (Maris & Oostenveld, 2007). This process was used for both the the 3-30 Hz ROI
analyses (where clusters were determined according to neighbouring timepoints and frequencies)
and the whole scalp analysis using IAF (where clusters were determined according to
neighbouring locations and timepoints). FieldTrip could not be used to test the 2 age (young, old)
x 2 voluntariness (voluntary, involuntary) fully between-subjects interaction. Thus, STATSLAB
(Campopiano et al., 2018) was used for this comparison. For this analysis, the distribution of
difference scores was generated through a bootstrapping procedure with 1000 iterations,
differences across the entire time window were evaluated (-1 s to 3 s) and corrected for multiple
comparisons with the Benjamini-Hochberg procedure for correction (Benjamini & Hochberg,
1995).

3. Results

3.1 Behavioural

3.1.1 Sound Localization Accuracy

Accuracy on the cover task (sound localization) was analyzed using a 2 Age (young, old)
x 2 Voluntariness (voluntary, involuntary) between-subjects analysis ANOVA. The ANOVA
revealed a significant main effect of age, $F(1, 64) = 4.13$, $p = .044$, $\eta^2 = .065$, such that older
adults (M = 0.73, SD = 0.29) were less accurate on average than younger adults (M = 0.87, SD =
0.23). There was no significant main effect of voluntariness, $F(1, 64) = 0.44$, $p = .511$, and no
age by voluntariness interaction, $F(1, 64) = 0.72$, $p = .400$. Thus, younger adults had better

performance on the sound localization cover task than older adults, but voluntariness of retrieval did not influence cover task performance.

3.1.2 Sound Localization Reaction Times

If participants were engaged in memory retrieval (either voluntary or involuntary) during sound localization, then we might expect slower RTs for paired than unpaired sounds (as only the former should bring an associated picture to mind). Additionally, we might expect slower RTs for voluntary compared to involuntary retrieval reflecting the additional effortful processing. To test this, sound localization RTs from correct trials only were submitted to a 2 Age (young, old) x 2 Voluntariness (voluntary, involuntary) x 2 Sound type (paired, unpaired) mixed ANOVA (see Figure 2). The main effect of age was not significant, $F(1, 46) = 2.53$, $p = .118$, $\eta^2 = .052$, while the main effect of voluntariness was significant, $F(1, 46) = 4.99$, $p = .030$, $\eta^2 = .098$, with slower RTs during voluntary (M = 526.6 ms, SD = 83.82 ms) than involuntary (M = 473.3 ms, SD = 84.85 ms) retrieval. Moreover, there was a main effect of sound type, $F(1, 46) = 6.56$, $p = .014$, $\eta^2 = .125$, such that participants were slower to respond to paired (M = 505.9, SD = 87.20) than unpaired (M = 494.0, SD = 84.66) sounds. None of the interactions were significant: age x voluntariness, $F(1, 46) = 0.64$, $p = .427$; voluntariness x sound type, $F(1, 46) = 1.80$, $p = .186$; age x sound type, $F(1, 46) = 1.62$, $p = .209$; age x voluntariness x sound type, $F(1, 46) = 0.60$, $p = .808$. Thus, participants were slower on average to respond on trials that were originally paired with an image at encoding compared to unpaired trials, suggesting that bringing the image to mind (at least on some trials) may have interfered with/slowed their localization response, as did having the intention to retrieve.
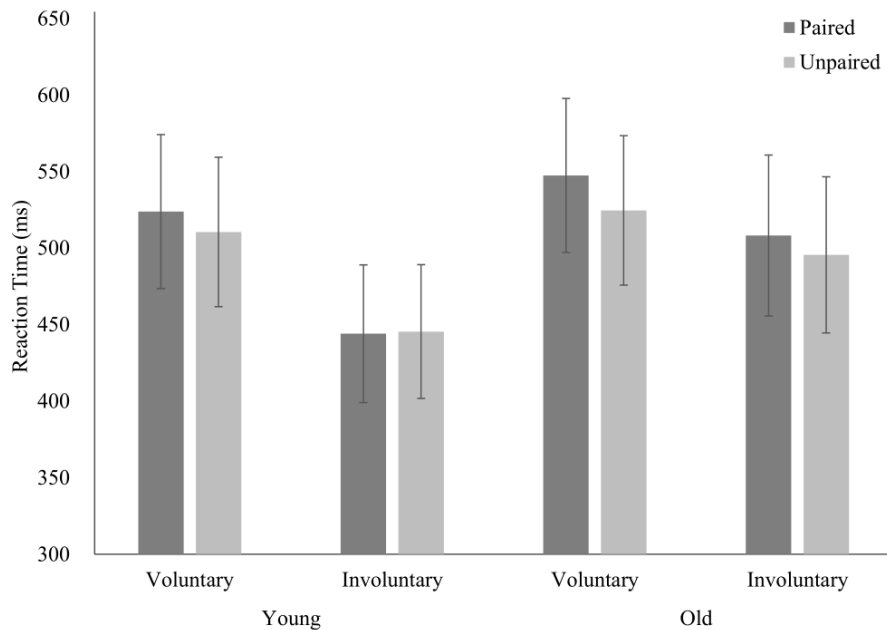
Figure 2. Reaction times for the sound localization task separated by age group and voluntariness condition. Error bars represent 95% CI. Effects separated for paired and unpaired trials. A main effect of sound type was observed such that paired trials had slower reaction times than those with no associated image (*p* = .014). A main effect of voluntariness was also observed such that responses were slower during voluntary than involuntary retrieval (*p* = .030).

3.1.3 Explicit Memory Performance

3.1.3.1 Paired Sounds

To determine whether age and retrieval intention affected the number of memories participants reported having for paired sounds during the sound localization task, retrospective "yes" responses for paired sounds were submitted to a 2 Age (young, old) x 2 Voluntariness (voluntary, involuntary) between-subjects ANOVA (see Table 2 for means). The ANOVA revealed a significant main effect of age, $F(1, 62) = 27.32$, $p < .001$, $\eta^2 = .303$, but no effect of voluntariness, $F(1, 62) = 0.01$, $p = .931$, and no interaction between age and voluntariness, $F(1,$

62) = .821, p = .368. Older adults reported fewer memories for paired sounds than younger

adults overall, $t(64)$ = 1.84, $p < .001$ (see Table 2).

3.1.3.2 Unpaired Sounds

Reporting a memory for an unpaired sound during the retrospective memory task could

be considered a false alarm, since these sounds did not have pictures associated with them at

encoding and so should not have elicited a visual memory. These false alarms were submitted to

a 2 Age (young, old) x 2 Voluntariness (voluntary, involuntary) between-subjects ANOVA (see

Table 2 for means). The ANOVA revealed a significant main effect of age, $F(1, 62)$ = 20.56, $p <$

.001, η^2 = .245, but no effect of voluntariness, $F(1, 62)$ = 1.02, p = .318, and no age by

voluntariness interaction, $F(1, 62)$ = 0.24, p = .625. As shown in Table 2, older adults made

more false alarms to unpaired sounds than younger adults, t = 4.53, $p < .001$, saying that they had

recalled a picture when they heard the sound, even though that was not possible (or at least, they

could not have remembered a picture from the encoding phase).

3.1.3.3 Final Cued Recall

The number of correctly recalled pictures on the final cued recall task was submitted to a

2 Age (young, old) x 2 Voluntariness (voluntary, involuntary) between-subjects ANOVA (See

Table 2 for means). There was a significant main effect of age, $F(1, 62)$ = 63.93, $p < .001$, η^2 =

.504, no effect of voluntariness, $F(1, 62)$ = .845, p = .362, and no age by voluntariness

interaction, $F(1, 62)$ = 0.16, p = .691. Unsurprisingly, younger adults successfully recalled more

pictures in response to the sounds on the final cued recall task than older adults, $t(64)$ = 8.09, $p <$

001.

Table 2. *Explicit Memory Performance of Young and Older Adults in Voluntary and Involuntary Retrieval Conditions.*

	Young Adults				Older Adults				t
	Overall (M(SD))	Voluntary (M(SD))	Involuntary (M(SD))	t	Overall (M(SD))	Voluntary (M(SD))	Involuntary (M(SD))	t	
Paired said recalled	43.7(4.77)	42.9(4.83)	44.4(4.75)	0.56	34.1(9.07)	35.0(7.81)	33.2(10.4)	0.73	5.23**
Unpaired said recalled (i.e. false alarms)	5.50(5.34)	6.00(5.46)	5.00(5.34)	0.36	14.3(9.46)	15.7(9.78)	12.9(9.15)	1.09	4.53**
Correctly recalled on final cued recall task	39.5(7.14)	39.0(7.73)	40.1(6.76)	0.36	23.2(9.08)	21.8(8.55)	24.53(9.66)	-0.96	7.99**

**p<.001

3.2 EEG

3.2.1 Voluntariness Effects

3.2.1.1 Voluntariness by Age

The effects of retrieval intention and age were first examined by submitting time frequency data from the occipital and frontal ROIs (for paired sounds only) to two separate 2 Age (young, old) x 2 Voluntariness (voluntary, involuntary) between-subjects analyses (see Methods for details). These analyses revealed significant interactions in the alpha frequency range (approximately 8-12 Hz) at both predefined ROIs (see Figures 3B and E). Younger adults showed significantly greater alpha ERD during voluntary than involuntary retrieval at both frontal (Figure 3A) and occipital (Figures 3D) ROIs. In contrast, older adults showed similar

patterns of activity between voluntariness conditions at frontal (Figure 3C) and occipital (Figure

3F) ROIs. This enhanced ERD during involuntary retrieval for older adults was present between

400 to 2300ms post-stimulus onset at frontal (Figure 3C) and 450 to 2500ms post-stimulus onset

at occipital (Figure 3E) ROIs. We followed up on the significant voluntariness by age interaction

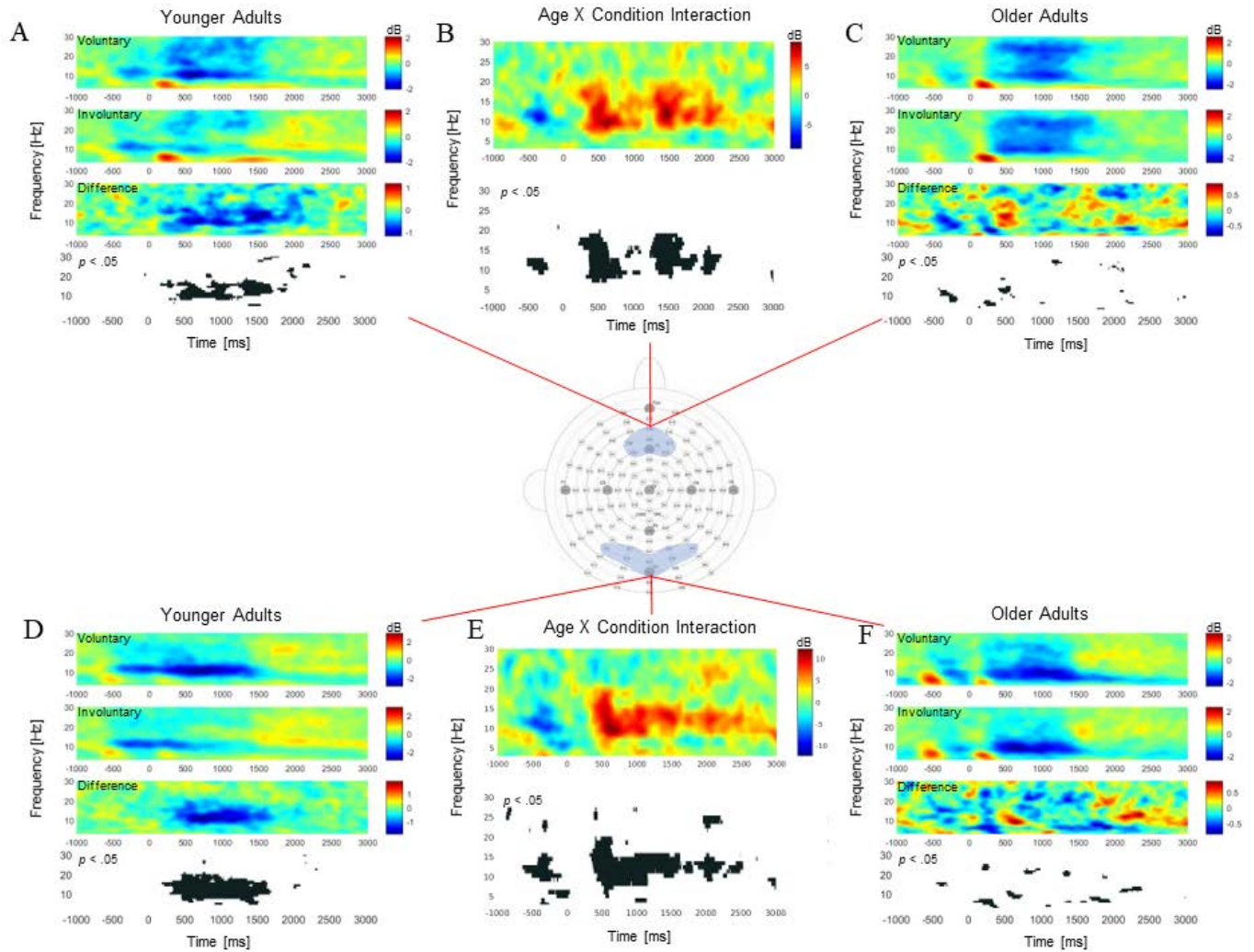by examining the effect of age within the voluntary and involuntary groups separately.

Figure 3. Time-frequency plots of the interaction between voluntariness and age at the frontal

and occipital ROIs. A. Activity in voluntary and involuntary conditions in younger adults at the

frontal ROI with difference plot showing the difference in activity between voluntariness

conditions (voluntary-involuntary), and plot showing statistically significant points in black (*p* <

.05, after Benjamini-Hochberg correction). B. Age by Condition interaction ((voluntary old-voluntary young)-(involuntary old-involuntary young)) plotted as differences over all frequencies analysed at the frontal ROI. Plot showing statistically significant points in the above plot in black ($p < .05$ corrected). C. Same plots as A showing data from older adults at frontal ROI. D. Same plots as A showing data from younger adults at occipital ROI. E. Same interaction plots as B showing data from occipital ROI. E. Same plots as A showing data from older adults at occipital ROI.

3.2.1.2 Voluntary

In the ROI analyses, the occipital ROI assessed across all frequencies did not significantly differ when comparing older and younger adults in the voluntary condition ($ps \geq$ .105), suggesting that older and younger adults similarly engaged occipital regions under the voluntary retrieval condition. There were also no age differences in the frontal ROI across all frequencies ($ps \geq .214$), suggesting that older and younger adults similarly activated frontal regions under voluntary retrieval conditions. Further supporting these findings, IAF analyses applied across the whole scalp, showed no significant age effects in the voluntary condition ($ps \geq .115$). In Figure 3, similar response patterns can be seen for both age groups in the voluntary condition between 3-30 Hz.

3.2.1.3 Involuntary

A significant difference between young and older adults was observed at the mid-frontal ROI. This difference was driven by a cluster in the high alpha to beta range, spanning from 500 ms to 2400 ms post stimulus onset ($p = .003$; see Figures 4A and B). Additionally, we identified a significant difference between young and older adults at the occipital ROI ($p = .044$). This difference was driven by a later cluster in the alpha range, spanning from 1600 ms to 3000 ms

post stimulus onset (see Figures 4C and D). Whole-scalp IAF analyses revealed a similar pattern

of results with frontal and occipital clusters showing greater alpha ERD in older adults between

1400 ms and 3000 ms post stimulus (*p*=.003; Figure S1), suggesting this effect was not driven by

age differences in peak alpha frequency. Taken together, these results suggest that older adults

show greater engagement of frontal and occipital regions than younger adults during involuntary
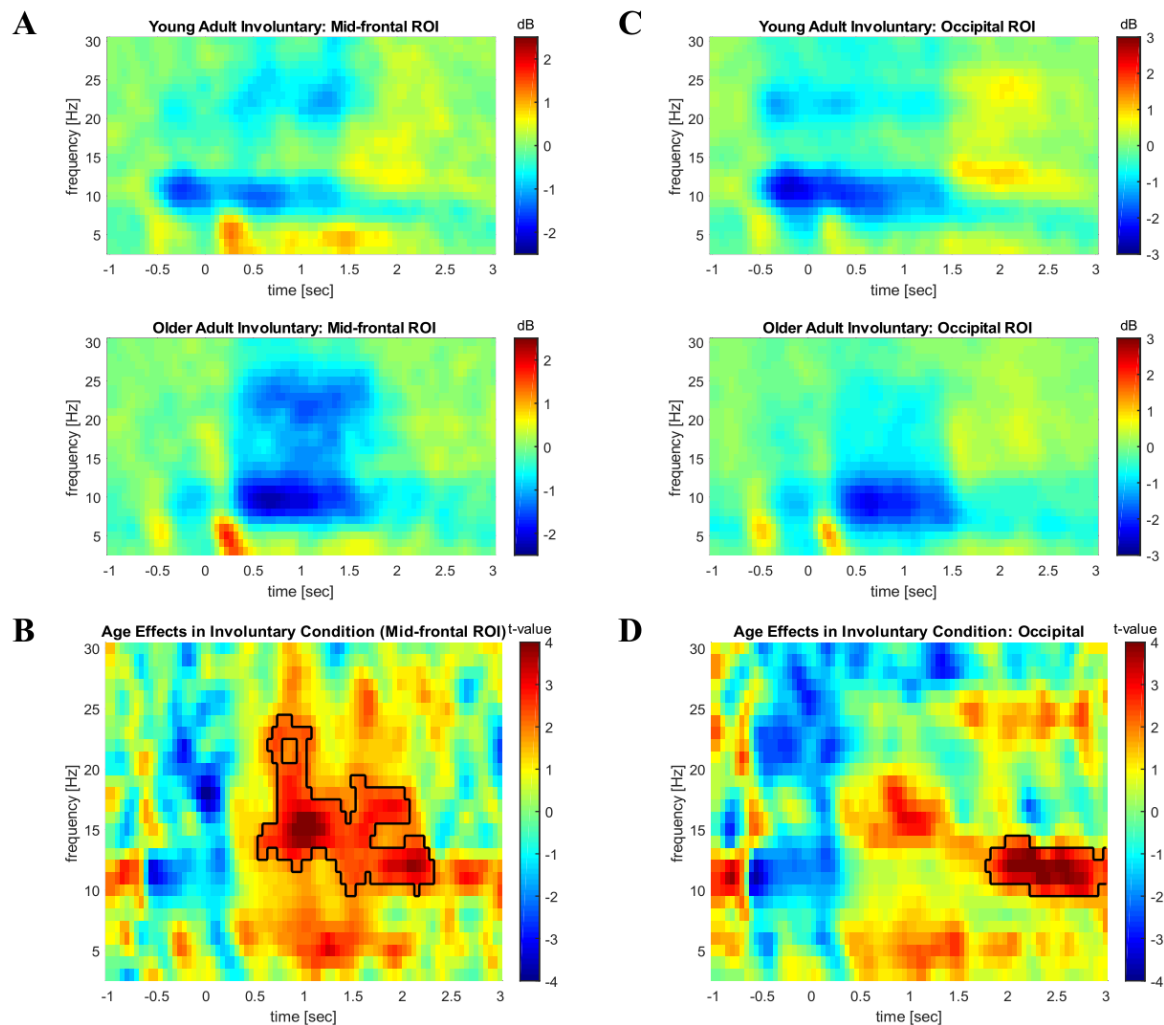
retrieval.

Figure 4. Age differences during involuntary retrieval. A. Time frequency plots for the frontal
ROI in young and older adults relative to pre-fixation baseline. B. Outlined cluster showing
significantly greater ERD in older than younger adults in the alpha/beta range for the frontal ROI

(p = .003). C. Time frequency plots for the occipital ROI in young and older adults relative to pre-fixation baseline. D. Outlined cluster showing significantly greater ERD in older than younger adults in the alpha/beta range for the occipital ROI late in the trial (p = .044).

3.2.2 Sound Type Effects

3.2.2.1 Sound Type by Age

We expected greater alpha desynchrony for paired than unpaired sounds during the sound localization task, reflecting reactivation of the associated pictures in visual regions. We first examined the effect of sound type in younger and older adults together by submitting the time frequency data from the occipital and frontal ROIs to separate 2 Age (young, old) x 2 Sound Type (paired, unpaired) mixed analyses with cluster correction such that p-values represent the significance value of the largest cluster. The main effect of sound type (frontal: ps >= .765; occipital: ps >= .646) was not significant, nor was the age x sound type interaction (frontal: ps >= .603; occipital: ps >= .291). This was not a product of collapsing across retrieval intention groups, as we also did not observe sound type or interaction effects in the voluntary (frontal: ps >= .354; occipital: ps >= .469) and involuntary (frontal: ps >= .525; occipital: ps >= .361) groups alone. A similar pattern of results was observed using IAFs (all participants, main effect of sound type: ps >= .249). Nevertheless, we next performed planned comparisons within each age group separately as previous work suggests that the timing and pattern of oscillatory memory effects can differ between groups (e.g., Karrasch et al., 2004).

3.2.2.2 Young

In young adults, we found no significant differences between paired and unpaired trials at both frontal (ps >= .869) and occipital ROIs (ps >= .215; Figure 5B) across all frequencies assessed (3-30 Hz). Moreover, there was no significant interaction between voluntariness and

sound type within either of the regions of interest (mid frontal, ps > .374; or occipital, ps >= .464).

3.2.2.3 Old

In older adults, we found a significant difference between paired and unpaired trials in the occipital ROI, driven by a significant cluster in the alpha to low beta range with a time course between 1.5 s to 2.1 s post stimulus onset (p = .023) (Figure 5D). This effect was not significant at the mid-frontal ROI (ps > = .148). No interaction between voluntariness and sound type was observed in either the frontal (ps >= .415) or occipital ROIs (ps >= .593), suggesting that this memory-related ERD effect was similar for the older voluntary and involuntary retrieval groups.
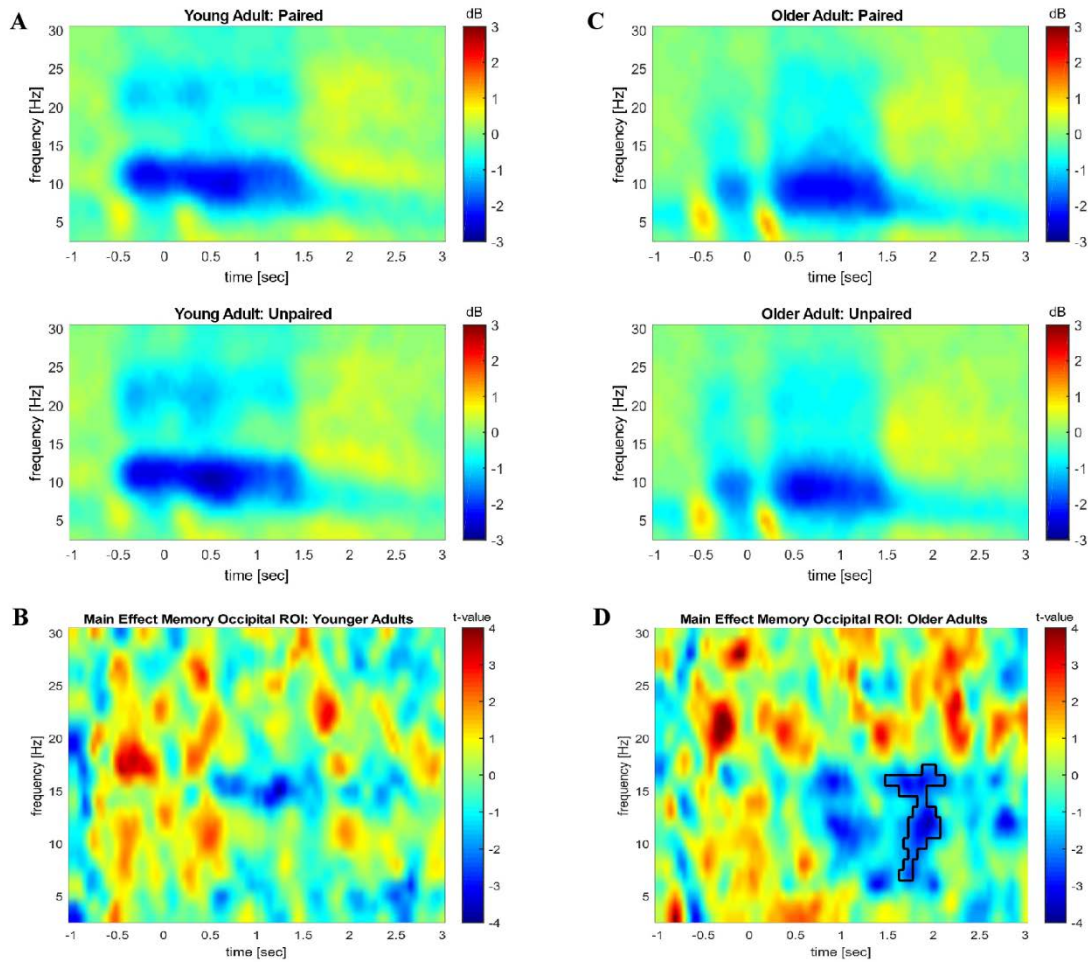
Figure 5. Time-frequency plots displaying memory-related differences separately in younger and older adults for the occipital ROI. A. Time-frequency plots of activity in paired (top) and unpaired (bottom) trials in young adults. B. Difference plot displaying t-values for the comparison between paired and unpaired trials in younger adults, no significant effects are observed. C. Time-frequency plots of activity in paired (top) and unpaired (bottom) trials in older adults. D. Difference plot displaying t-values for the comparison between paired and unpaired trials in older adults. Outlined cluster shows relative ERD in the alpha and beta range was significantly greater for paired than unpaired sounds ($p = .023$).

3.2.3 Hearing and Alpha

Finally, to rule out the possibility that age differences in alpha desynchrony were caused

by hearing loss (Petersen et al., 2015; Peelle & Wingfield, 2016), we examined whether

participants' scores on the Hearing Inventory Scale correlated with alpha ERD (using IAF across

all sites and the entire trial length for paired trials only) separately in our young and older adult

groups. In young adults, Hearing Inventory Scale scores did not correlate with alpha ERD in

either the voluntary ($ps >= .486$) or involuntary conditions ($ps >= .192$), or in the two groups

combined ($ps >= .434$). Similarly, Hearing Inventory Scale scores did not correlate with alpha

ERD in older adults in either the voluntary ($ps >= .232$) or involuntary ($ps >= .261$) conditions,

or in the two groups combined ($ps >= .163$).

4 Discussion

This study expands on past literature by examining age differences in the neural

underpinnings of involuntary memory, which is thought to place fewer demands on cognitive

control than voluntary memory (Schlagman et al., 2009; Berntsen et al., 2017). We investigated

the effects of age and voluntariness on memory performance and EEG activity using a paradigm

that involves retrieval of experimentally encoded sound-picture pairs. Reaction times collected

during the sound localization task showed that both age groups responded more slowly to paired

than unpaired sounds and during voluntary than involuntary retrieval – implicit measures of

retrieval success and enhanced retrieval effort, respectively. However, retrospective self-reports

showed fewer memories to paired sounds and more false memories for unpaired sounds in older

compared to younger adults, and no difference in memory performance according to

voluntariness condition. In terms of voluntariness effects in the EEG data, young adults showed

higher alpha ERD over frontal and occipital sites during voluntary than involuntary retrieval,

while older adults showed similarly high alpha ERD across both conditions. Analysis of sound type effects in EEG revealed that older, but not younger, adults exhibited the expected effect of increased alpha ERD over occipital sites in response to paired relative to unpaired sounds, suggesting that they reactivated the associated pictures at retrieval.

Young adults had diminished alpha ERD in both ROIs during involuntary retrieval compared to voluntary retrieval, replicating previous work showing that involuntary remembering requires less top-down control than voluntary remembering (e.g., Koechlin et al., 1999; Hall et al., 2014, Wang et al., 2016). In contrast, older adults showed equivalent levels of alpha ERD during both forms of retrieval, suggesting that even though involuntary retrieval requires less cognitive effort than voluntary retrieval, older adults still devoted additional neural resources to it. This finding is consistent with previous demonstrations of older adults over-activating frontal sites at lower levels of demand and then failing to increase any further as task demands continue to increase (e.g., Reuter-Lorenz & Cappell, 2008; Cappell et al., 2010; Toepper et al., 2014). While some studies suggest that increased frontal activation with age is compensatory, in that it relates to better performance (e.g., Morcom et al., 2007; Duverne et al., 2008), other studies fail to find this relationship, suggesting instead that frontal over-activation reflects (unsuccessful) attempts to compensate for limited resources (e.g., Cabeza, 2002; Duarte et al., 2006), or cortical dedifferentiation associated with poor efficiency (e.g., Cabeza, 2002; Morcom et al., 2003; Duverne et al., 2008; Morcom & Henson, 2018).

While older adults' increased alpha ERD during involuntary retrieval may reflect greater top-down control, a number of other possible explanations should be considered. First, it is possible that the similarly high alpha ERD across conditions in older adults reflects a lessened ability to modulate activity in these regions according to task demands (e.g., Morcom & Rugg,

2004; for a review, see Morcom, 2016). Alternatively, older adults' greater activity in the involuntary condition could reflect the dual task conditions (Collette et al., 2005), performance concerns (e.g. Barber & Mather, 2014; Ryan & Campbell, 2021), or subjectively greater task difficulty (Höller-Wallscheid et al., 2017). Another possibility is that older adults were experiencing more off-task thoughts during involuntary retrieval. However, this seems unlikely, given that older adults typically report fewer instances of mind-wandering than younger adults (e.g. Jackson & Balota, 2012; Frank et al., 2015), possibly due to their greater motivation (Seli et al., 2020; Ryan & Campbell, 2021). Moreover, older adults' higher alpha ERD in the involuntary condition was time-locked to the stimulus, not pervasive throughout the task as one might expect for mind-wandering. That said, we cannot rule out the possibility that older adults were experiencing other intrusive memories in response to the environmental sounds. Older adults did report having more images come to mind for the *unpaired* sounds than young adults, which we interpreted as a failure of metacognition. However, these 'false alarms' could reflect genuine intrusions of memories from outside the experiment due to poor inhibitory control. Indeed, reduced inhibitory control with age may actually contribute to the preservation of involuntary memory in everyday life, in that older adults may be less able to stop intrusive associations from coming to mind in response to environmental cues (e.g., Healey, Hasher, & Campbell, 2013). This question deserves further exploration.

One important difference between the current paradigm and previous work looking at involuntary memory and aging is that the current study involved a dual-task scenario, with the sound localization cover task coinciding with the main memory retrieval task. Dual-task conditions require divided attention and consistently relate to greater performance costs in older adults (McDowd & Craik, 1988; Fernandes & Moscovitch, 2003). Thus, the dual-task demands

may have been detrimental to performance, particularly in the older group, countering the expected preservation of involuntary memory with age and resulting in frontal over-activation during involuntary retrieval. While classical divided attention paradigms use secondary tasks that are outside the main focus of attention (e.g., monitoring a sequence of numbers for a target number while trying to encode and/or retrieve a list of words; Craik et al., 1996; Craik et al., 2018), here the additional memory retrieval demands were of theoretical interest. Thus, although there is no way to statistically separate the influence of dual-task vs retrieval demands in the current study, future work should compare the additional demands of voluntary retrieval with more traditional dual-task conditions.

Behaviourally, both age groups showed slower RTs on the sound localization cover task when retrieval was intentional and when the sound was associated with a picture. This suggests that as cognitive demands increased, localization response times slowed. This potential competition for attentional resources is consistent with work showing that the posterior parietal cortex, a region critical for attention, is similarly engaged during episodic retrieval and perceptual tasks (see Cabeza et al., 2008, for a review; Sestieri et al., 2017). Similarly, previous work suggests that RTs on perceptual tasks are slowed when they coincide with memory retrieval (Craik et al., 1996; Lozito & Mulligan, 2010). Thus, our RT measure provides valuable confirmation that both age groups were engaging with the retrieval task as expected and that the voluntariness manipulation was successful. Since self-report is notoriously inaccurate (e.g. Hermann, 1994) and metacognitive abilities are known to decline with age (Palmer et al., 2014), response time may therefore provide a more objective, accurate measure of retrieval effort/success than post-scan self-report measures.

We did not observe a difference in participants' retrospective reports of memory between the voluntary and involuntary conditions. This may have been due to poor metacognition, particularly in the older group (Palmer et al., 2014; Hertzog & Curley, 2018), potentially exacerbated by the fact that participants heard each sound twice during sound localization. Participants may have been confused if they experienced a memory for one of those instances, but not the other. Alternatively, the instructions given to the involuntary memory group (saying that it was okay if a memory came to mind spontaneously) may have biased participants' attention toward recalling pictures. However, our reaction time and EEG data suggest that both age groups differentiated between voluntary and involuntary conditions and critically, pilot testing suggested that this instruction was necessary to prevent suppression of retrieval in the involuntary group (Hall et al., 2014). Another factor that may have contributed to the seeming lack of preservation of involuntary memory in the older group was the type of memory being tested here. While previous work has primarily focused on autobiographical memory (Schlagman et al., 2009; Berntsen et al., 2015), the current study used paired associates which are particularly difficult for older adults to learn/recall (Old & Naveh-Benjamin, 2008). Given that age differences in associative memory are minimized when items are semantically related (e.g., Sharps & Antonelli, 1997), we used semantically related pairs to facilitate optimal performance in older adults. Despite this measure, older adults recalled fewer pairs on the final cued recall task, suggesting that even semantically related pairs may not come to mind as automatically as personally meaningful autobiographical memories (Berntsen, 2010).

In regard to the EEG sound type effects, older adults' increased occipital alpha ERD to paired relative to unpaired sounds suggests that they reactivated the visual memory in response to the associated sounds (Khader & Rösler, 2011; Waldhauser et al., 2012). Young adults did not

show this effect (though age differences should be interpreted with caution since the age x

memory interaction was not significant). There are several potential reasons why the sound type

effect was not significant in the younger group. First, most previous studies investigating ERD as

a neural correlate of memory retrieval have used voluntary retrieval tasks (for reviews, see:

Klimesch, 1999; Hanslmayr et al., 2012), which may yield a more robust memory effect. Second,

participants were exposed to the paired and unpaired sounds a different number of times at

encoding (4 repetitions for paired, 2 repetitions for unpaired). Previous work has shown that

repeated exposures to a stimulus can lead to increased alpha *synchrony* (e.g. Gilbert et al., 2010),

rather than desynchrony, and this may have worked against our ability to find an effect in the

younger group[1]. Third, the nature of the environmental sounds used in the present study may

have reduced the time locking of memory reactivation between trials, as well as across

individuals. Distinctive features of the sound vary throughout the entire sound duration, meaning

that even when retrieval is successful, the onset of that retrieval may differ across trials and

individuals. This in turn may have reduced the likelihood of finding memory effects in the EEG

signal, especially because involuntary retrieval can be quite short-lived (Berntsen et al., 2013;

Schlagman & Kvavilashvili, 2008). Finally, in order to equate trial numbers across age groups,

our memory analysis used *all* paired trials instead of only those that were later reported as

remembered, and this may have diluted the memory effect.

Given these potential limitations, it is remarkable that older adults showed increased

alpha ERD to paired sounds. This suggests that occipital alpha ERD may serve as a sensitive

measure of memory in older adults, and may be less susceptible to increased trial-by-trial latency

---

[1] This difference in exposure would have also worked against our ability to find a paired > unpaired difference in the older group, so this aspect of the design cannot explain the ERD effect in that group. Nor can it explain the finding of slower RTs to paired than unpaired sounds, which is the opposite of what would be expected from perceptual priming work (where greater exposure usually leads to faster responding; e.g., Bergerbest et al., 2004).

jitter observed in ERP studies of aging (Murray et al., 2019). Murray and colleagues (2019) suggested that interpreting ERPs in older adult may be problematic in that component onsets become more variable with age, serving to reduce and smear ERP amplitudes. While they showed that single-trial latency correction helps correct this issue, our data suggest that examining the spectral properties of ongoing EEG may similarly provide adequate sensitivity in data obtained from older adults. The present work, in conjunction with previous studies showing similar memory-related oscillatory activity in young and old at encoding (Strunk & Duarte, 2019) and retrieval (Karrasch et al., 2004; Allen et al., 2020), suggests that alpha ERD may be a particularly sensitive memory measure for use with older adults.

In summary, we observed behavioural markers of retrieval success and retrieval intentionality in both groups, as RTs were slower in response to paired than unpaired sounds and during voluntary than involuntary retrieval. We also found age differences in retrospective memory reports that did not differ according to the voluntariness of retrieval, though this may have been due to certain aspects of the design. Older adults showed similarly high alpha ERD during both voluntariness conditions reflecting overactivation even at relatively low levels of task demands, while young adults showed the expected increase in alpha ERD in voluntary retrieval alone. Future work may benefit from using more naturalistic stimuli, such as movies or narratives (Campbell et al., 2015, 2016), which are rich with meaning and emotion like everyday life, but conveniently can be used to study involuntary memory in the lab (e.g., Berntsen et al., 2017). Importantly, we also found that older, but not younger, adults showed increased alpha ERD for paired relative to unpaired sounds at occipital sites during retrieval, suggesting that changes in oscillatory power can also be used as a neural marker of memory reactivation in older adults.

Acknowledgements

References

Allen, J., Hellerstedt, R., Sharma, D., & Bergström, Z. M. (2020). Distraction by unintentional

recognition: Neurocognitive mechanisms and effects of aging. *Psychology and Aging,*

35(5), 639–653. https://doi.org/10.1037/pag0000398

Anderson, N. D., Craik, F. I. M., & Naveh-Benjamin, M. (1998). The attentional demands of

encoding and retrieval in younger and older adults: I. Evidence from divided attention

costs. *Psychology and Aging, 13*, 405–423. https://psycnet.apa.org/doi/10.1037/0882-

7974.13.3.405

Barber, S. J., & Mather, M. (2014). Stereotype threat in older adults: When and why does it

occur and who is most affected? In P. Verhaeghen & C. Hertzog (Eds.), *Oxford library of*

psychology. The Oxford handbook of emotion, social cognition, and problem solving in

adulthood (p. 302–319). Oxford University Press.

https://doi.org/10.1093/oxfordhb/9780199899463.013.008

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and

powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B*

(Methodological), *57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bergerbest, D., Ghahremani, D. G., & Gabrieli, J. D. (2004). Neural correlates of auditory

repetition priming: reduced fMRI activation in the auditory cortex. *Journal of cognitive*

neuroscience, *16*(6), 966–977. https://doi.org/10.1162/0898929041502760

Bergström, Z., Williams, D., Bhula, M., & Sharma, D. (2016). Unintentional and intentional

recognition rely on dissociable neurocognitive mechanisms. *Journal of Cognitive*

Neuroscience, *28*, 1838-1848. https://doi.org/10.1162/jocn_a_01010

Berntsen, D. (1996). Involuntary autobiographical memories. *Applied Cognitive Psychology, 10*, 435–454. https://doi.org/10.1002/(SICI)1099-0720(199610)10:5%3C435::AID-ACP408%3E3.0.CO;2-L

Berntsen, D. (2010). The unbidden past: Involuntary autobiographical memories as a basic mode of remembering. *Current Directions in Psychological Science*, *19*(3), 138–142. https://doi.org/10.1177/0963721410370301

Berntsen, D., Rasmussen, A. S., Miles, A. N., Nielsen, N. P., & Ramsgaard, S. B. (2017). Spontaneous or intentional? Involuntary versus voluntary episodic memories in older and younger adults. *Psychology and Aging, 32*(2), 192-201. https://psycnet.apa.org/doi/10.1037/pag0000157

Berntsen, D., Rubin, D. C., & Salgado, S. (2015). The frequency of involuntary autobiographical memories and future thoughts in relation to daydreaming, emotional distress, and age. *Consciousness and Cognition, 36*, 352–372. https://psycnet.apa.org/doi/10.1016/j.concog.2015.07.007

Berntsen, D., Staugaard, S. R., & Sørensen, L. M. T. (2013). Why am I remembering this now? Predicting the occurrence of involuntary (spontaneous) episodic memories. *Journal of Experimental Psychology: General, 142*(2), 426–444. https://psycnet.apa.org/doi/10.1037/a0029128

Burgess, A. P., & Gruzelier, J. H. (2000) Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*, 596–606. https://doi.org/10.1111/1469-8986.3750596

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD

    model. *Psychology and Aging, 17*(1), 85–100. https://psycnet.apa.org/doi/10.1037/0882-

    7974.17.1.85

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and

    episodic memory: an attentional account. *Nature Reviews Neuroscience*, *9*(8), 613–625.

    https://doi.org/10.1038/nrn2459

Campbell, K. L., Samu, D., Davis, S. W., Geerligs, L., Mustafa, A., & Tyler, L. K. for Cam-

    CAN (2016). Robust resilience of the frontotemporal syntax system to aging. *Journal of*

    Neuroscience, 36, 5214-5227. https://doi.org/10.1523/JNEUROSCI.4561-15.2016

Campbell, K. L., Shafto, M. A., Wright, P., Tsvetanov, K. A., Geerligs, L., Cusack, R., Cam-

    CAN, & Tyler, L. K. (2015). Idiosyncratic responding during movie-watching predicted

    by age differences in attentional control. *Neurobiology of Aging, 36*, 3045-3055.

    https://doi.org/10.1016/j.neurobiolaging.2015.07.028

Campopiano, A., Noordt, S. J. V., & Segalowitz, S. J. (2018). STATSLAB: An open-source

    EEG toolbox for computing single-subject effects using robust statistics. *Behavioural*

    Brain Research, *347*, 425–435. https://doi.org/10.1016/j.bbr.2018.03.025

Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls

    spatial attention through modulation of anticipatory alpha rhythms. Journal of

    Neuroscience, 29(18), 5863-5872. https://doi.org/10.1523/JNEUROSCI.0539-09.2009

Cappell, K. A., Gmeindl, L., & Reuter-Lorenz, P. A. (2010). Age differences in prefrontal

    recruitment during verbal working memory maintenance depend on memory

    load. *Cortex*, *46*(4), 462–473. https://doi.org/10.1016/j.cortex.2009.11.009

Collette, F., Olivier, L., Linden, M. V., Laureys, S., Delfiore, G., Luxen, A., & Salmon, E. (2005). Involvement of both prefrontal and inferior parietal cortex in dual-task performance. *Cognitive Brain Research, 24*(2), 237-251. https://doi.org/10.1016/j.cogbrainres.2005.01.023

Coren, S., & Hakstian, A. R. (1992). The development and cross-validation of a self-report inventory to assess pure-tone threshold hearing sensitivity. *Journal of Speech Language and Hearing Research, 35*(4), 921. https://doi.org/10.1044/jshr.3504.921

Craik, F. I., & Byrd, M. (1982). Aging and cognitive deficits. *Aging and Cognitive Processes,* 191-211. https://doi.org/10.1007/978-1-4684-4178-9_11

Craik, F. I. M., Govoni, R., Naveh-Benjamin, M., & Anderson, N. D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General, 125*, 159–180. https://psycnet.apa.org/doi/10.1037/0096-3445.125.2.159

Craik, F. I. M., Eftekhari, E. & Binns, M. A. (2018). Effects of divided attention at encoding and retrieval: Further data. *Memory & Cognition, 46***,** 1263–1277. https://doi.org/10.3758/s13421-018-0835-3

Curran, T. (1999). The electrophysiology of incidental and intentional retrieval: ERP old new effects in lexical decision and recognition memory. Neuropsychologia, 37, 771–785. https://psycnet.apa.org/doi/10.1016/S0028-3932(98)00133-X

Desjardins, J. A., Noordt, S. V., Huberty, S., Segalowitz, S. J., & Elsabbagh, M. (2021). EEG Integrated Platform Lossless (EEG-IP-L) pre-processing pipeline for objective signal

quality assessment incorporating data annotation and blind source separation. *Journal of Neuroscience Methods, 347*, 108961. doi:10.1016/j.jneumeth.2020.108961

Desjardins, J. A., & Segalowitz, S. J. (2013). Deconstructing the early visual electrocortical responses to face and house stimuli. *Journal of Vision., 13*(5), 1–18. https://doi.org/10.1167/13.5.22

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia, 41,* 318–333. https://psycnet.apa.org/doi/10.1016/S0028-3932(02)00164-1

Duarte, A., Ranganath, C., Trujillo, C., & Knight, R. T. (2006). Intact recollection memory in high-performing older adults: ERP and behavioral evidence. *Journal of Cognitive Neuroscience*, *18*(1), 33–47. https://doi.org/10.1162/089892906775249988

Duverne, S., Habibi, A., & Rugg, M. D. (2008). Regional specificity of age effects on the neural correlates of episodic retrieval. *Neurobiology of Aging, 29*, 1902–1916. https://psycnet.apa.org/doi/10.1016/j.neurobiolaging.2007.04.022

Ebbinghaus, H. (2013). Memory: a contribution to experimental psychology. *Annals of neurosciences*, *20*(4), 155–156. (Original work published 1885). https://doi.org/10.5214/ans.0972.7531.200408

Fernandes, M. A., & Moscovitch, M. (2003). Interference effects from divided attention during retrieval in younger and older adults. *Psychology and Aging, 18*(2), 219-230. https://psycnet.apa.org/doi/10.1037/0882-7974.18.2.219

Frank, D. J., Nara, B., Touron, D. R., & Kane, M. J. (2015). Validating older adults' reports of

    less mind-wandering: An examination of eye movements and dispositional influences.

    Psychology and Aging, 30(2), 266–278. doi:10.1037/pag0000031

Friedman, D. (2013). The cognitive aging of episodic memory: A view based on the event-

    related brain potential. *Frontiers in Behavioral Neuroscience*, *7*, 111.

    https://doi.org/10.3389/fnbeh.2013.00111

Friedman, D., Chastelaine, M. D., Nessler, D., & Malcolm, B. (2010). Changes in familiarity and

    recollection across the lifespan: An ERP perspective. *Brain Research*, *1310*, 124–141.

    https://doi.org/10.1016/j.brainres.2009.11.016

Grady, C. (2012) The cognitive neuroscience of ageing. *Nature Reviews Neuroscience, 13*, 491–

    505. https://doi.org/10.1038/nrn3256

Grandy, T. H., Werkle-Bergner, M., Chicherio, C., Schmiedek, F., Lövdén, M., & Lindenberger,

    U. (2013). Peak individual alpha frequency qualifies as a stable neurophysiological trait

    marker in healthy younger and older adults. *Psychophysiology*, *50*(6), 570–582.

    https://doi.org/10.1111/psyp.12043

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., &

    Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus-specific

    information. *ELife, 8*. doi:10.7554/elife.49562

Hall, S. A., Rubin, D. C., Miles, A., Davis, S. W., Wing, E. A., Cabeza, R., & Berntsen, D.

    (2014). The neural basis of involuntary episodic memories. *Journal of Cognitive

    Neuroscience*, *32*(5), 519-532. https://doi.org/10.1162/jocn_a_00633

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and episodic memory:

    Addressing the synchronization/desynchronization conundrum. *Trends in*

    Neurosciences, *39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Hanslmayr, S., Staudigl, T., & Fellner, M. C. (2012). Oscillatory power decreases and long-term

    memory: the information via desynchronization hypothesis. *Frontiers in Human*

    Neuroscience, *6*. https://doi.org/10.3389/fnhum.2012.00074

Healey, M. K., Hasher, L., & Campbell, K. L. (2013). The role of suppression in resolving

    interference: Evidence for an age-related deficit. *Psychology and Aging, 28*(3), 721–

    728. https://doi.org/10.1037/a0033003

Hermann, D. J. (1994). The validity of retrospective reports as a function of the directness of

    retrieval processes. In: Schwartz, N, Sudman, S. (eds) *Autobiographical memory and the*

    validity of retrospective reports (21–37). Springer, New York,

    NY. https://doi.org/10.1007/978-1-4612-2624-6_3

Hertzog, C., & Curley, T. (2018). Metamemory and Cognitive Aging. *Oxford Research*

    Encyclopedia of Psychology. https://doi/10.1093/acrefore/9780190236557.013.377

Höller-Wallscheid, M. S., Thier, P., Pomper, J. K., & Lindner, A. (2017). Bilateral recruitment of

    prefrontal cortex in working memory is associated with task demand but not with

    age. *Proceedings of the National Academy of Sciences, 114*(5).

    https://doi.org/10.1073/pnas.1601983114

Jackson, J. D., & Balota, D. A. (2012). Mind-wandering in younger and older adults: Converging

    evidence from the sustained attention to response task and reading for comprehension.

    Psychology and Aging, 27(1), 106–119. doi: 10.1037/a0023933

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional

uses of memory. *Journal of Memory and Language*, *30*(5), 513–541.

https://doi.org/10.1016/0749-596X(91)90025-F

James, T., Strunk, J., Arndt, J., & Duarte, A. (2016). Age-related deficits in selective attention

during encoding increase demands on episodic reconstruction during context retrieval:

An ERP study. *Neuropsychologia, 86*, 66–79.

https://doi.org/10.1016/j.neuropsychologia.2016.04.009

Jennings, J. M., & Jacoby, L. L. (1993). Automatic versus intentional uses of memory: Aging,

attention, and control. *Psychology and Aging, 8*(2), 283–293.

https://doi.org/10.1037/0882-7974.8.2.283

Karrasch, M., Laine, M., Rapinoja, P., & Krause, C. M. (2004). Effects of normal aging on

event-related desynchronization/synchronization during a memory task in

humans. *Neuroscience Letters, 366*(1), 18-23.

https://doi.org/10.1016/j.neulet.2004.05.010

Khader, P. H., and Rösler, F. (2011). EEG power changes reflect distinct mechanisms during

long-term memory retrieval. *Psychophysiology, 48*, 362–369.

https://doi.org/10.1111/j.1469-8986.2010.01063.x

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory

performance: a review and analysis. *Brain Research Reviews*, *29*(2-3), 169–195.

https://doi.org/10.1016/S0165-0173(98)00056-3

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored

information. *Trends in Cognitive Sciences*, *16*(12), 606–617.

https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–

timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://

https://doi.org/10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schimke, H., Doppelmayr, M., Ripper, B., Schwaiger, J., and Pfurtscheller, G.

(1996). Event-related desynchronization (ERD) and the Dm effect: Does alpha

desynchronization during encoding predict later recall performance? *International*

Journal of Psychophysiology, 24, 47–60. https://psycnet.apa.org/doi/10.1016/S0167-

8760(96)00054-2

Knyazeva, M. G., Barzegaran, E., Vildavski, V. Y., & Demonet, J. F. (2018). Aging of human

alpha rhythm. *Neurobiology of Aging*, *69*, 261–273.

https://doi.org/10.1016/j.neurobiolaging.2018.05.018

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior

prefrontal cortex in human cognition. *Nature, 399*, 148–151.

https://psycnet.apa.org/doi/10.1038/20178

Kompus, K., Eichele, T., Hugdahl, K., & Nyberg, L. (2011). Multimodal imaging of incidental

retrieval: The low route to memory. *Journal of Cognitive Neuroscience, 23*(4), 947-960.

https://doi.org/10.1162/jocn.2010.21494

Lozito, J. P., & Mulligan, N. W. (2010). Exploring the role of attention during implicit memory retrieval. *Journal of Memory and Language, 63*(3), 387-399. https://doi.org/10.1016/j.jml.2010.06.007

Maillet, D., & Schacter, D. L. (2016). From mind wandering to involuntary retrieval: Age-related differences in spontaneous cognitive processes. *Neuropsychologia*, *80*, 142–156. http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.017

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

McDowd, J. M., & Craik, F. I. M. (1988). Effects of aging and task difficulty on divided attention performance. *Journal of Experimental Psychology: Human Perception and Performance, 14*(2), 267-280. http://dx.doi.org/10.1037/0096-1523.14.2.267

Misselhorn, J., Friese, U., & Engel, A. K. (2019). Frontal and parietal alpha oscillations reflect attentional modulation of cross-modal matching. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-41636-w

Morcom, A. M. (2016). Mind Over Memory: Cuing the Aging Brain. *Current Directions in Psychological Science*, *25*(3), 143–150. https://doi.org/10.1177/0963721416645536

Morcom, A. M., Good, C. D., Frackowiak, R.S., & Rugg, M. D. (2003). Age effects on the neural correlates of successful memory encoding. *Brain, 126*, 213–229. https://doi.org/10.1093/brain/awg020

Morcom, A. M., & Henson, R. (2018). Increased prefrontal activity with aging reflects

nonspecific neural responses rather than compensation. *The Journal of neuroscience: the

official journal of the Society for Neuroscience*, *38*(33), 7303–7313.

https://doi.org/10.1523/JNEUROSCI.1701-17.2018

Morcom, A. M., Li, J., & Rugg, M. D. (2007). Age effects on the neural correlates of episodic

retrieval: Increased cortical recruitment with matched performance. *Cerebral.

Cortex 17*(11), 2491–2506. https://psycnet.apa.org/doi/10.1093/cercor/bhl155

Morcom, A. M., & Rugg, M. D. (2004). Effects of age on retrieval cue processing as revealed by

ERPs. *Neuropsychologia, 42*(11), 1525–1542.

https://doi.org/10.1016/j.neuropsychologia.2004.03.009

Murray, J. G., Ouyang, G., & Donaldson, D. I. (2019). Compensation of trial-to-trial latency

jitter reveals the parietal retrieval success effect to be both variable and thresholded in

older adults. *Frontiers in Aging Neuroscience*, *11*, 179.

https://doi.org/10.3389/fnagi.2019.00179

Nasreddine, Z. S., Phillips, N. A., Bã Dirian, V., Charbonneau, S., Whitehead, V., Collin, I., et

al. (2005). The Montreal cognitive assessment, MoCA: A brief screening tool for mild

cognitive impairment. *Journal of the American Geriatrics Society, 53*(4), 695-699.

https://doi.org/10.1111/j.1532-5415.2005.53221.x

Nessler, D., Friedman, D., Johnson, R., & Bersick, M. (2007). Does repetition engender the same

retrieval processes in young and older adults? *NeuroReport*, *18*(17), 1837–1840.

https://doi.org/10.1097/WNR.0b013e3282f16d9f

Niziurski, J. A., & Berntsen, D. (2019). Involuntary versus voluntary episodic memories: The

    effects of encoding factors and emotion. *Psychology of Consciousness: Theory,*

    Research, and Practice. https://doi.org/10.1037/cns0000190

Old, S. R., & Naveh-Benjamin, M. (2008). Differential effects of age on item and associative

    measures of memory: A meta-analysis. *Psychology and Aging, 23*(1), 104–

    118. https://doi.org/10.1037/0882-7974.23.1.104

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software

    for advanced analysis of MEG, EEG, and invasive electrophysiological

    data. *Computational Intelligence and Neuroscience*, 1–9.

    https://doi.org/10.1155/2011/156869

Palmer, E. C., David, A. S., & Fleming, S. M. (2014). Effects of age on metacognitive

    efficiency. *Consciousness and cognition*, *28*(100), 151–160.

    https://doi.org/10.1016/j.concog.2014.06.007

Parvaz, M. A., MacNamara, A., Goldstein, R. Z., & Hajcak, G. (2012). Event-related induced

    frontal alpha as a marker of lateral prefrontal cortex activation during cognitive

    reappraisal. *Cognitive, affective & behavioral neuroscience*, *12*(4), 730–740.

    https://doi.org/10.3758/s13415-012-0107-9

Peelle, J. E., & Wingfield, A. (2016). The neural consequences of age-related hearing loss.

    Trends in Neurosciences 39, 486–497.

    https://psycnet.apa.org/doi/10.1016/j.tins.2016.05.001

Peng, W., Hu, Y., Mao, Y., & Babiloni, C. (2015). Widespread cortical α-ERD accompanying visual oddball target stimuli is frequency but non-modality specific. *Behavioural brain research*, *295*, 71–77. https://doi.org/10.1016/j.bbr.2015.04.051

Pernet, C., Latinus, M., Nichols, T., & Rousselet, G. (2015). Cluster-based computational methods for mass univariate analyses of event-related brain potentials/fields: A simulation study. *Journal of Neuroscience Methods*, *250*, 85–93. https://doi.org/10.1016/j.jneumeth.2014.08.003

Petersen, E. B., Wöstmann, M., Obleser, J., Stenfelt, S., & Lunner, T. (2015). Hearing loss impacts neural alpha oscillations under adverse listening conditions. *Frontiers in Psychology*, *6,* 177. https://doi.org/10.3389/fpsyg.2015.00177

Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD) during visual processing. *International Journal of Psychophysiology, 16*(2-3), 147–153. https://doi.org/10.1016/0167-8760(89)90041-X

Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*(3), 177–182. https://doi.org/10.1111/j.1467-8721.2008.00570.x

Rubin, D.C., Berntsen, D. (2009). The frequency of voluntary and involuntary autobiographical memories across the life span. *Memory & Cognition, 37,* 679–688. https://doi.org/10.3758/37.5.679

Ryan, A. D., Campbell, K. L. (2021). The ironic effect of older adults' increased task motivation: Implications for neurocognitive aging. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-021-01963-4

Schlagman, S., & Kvavilashvili, L. (2008). Involuntary autobiographical memories in and

    outside the laboratory: How different are they from voluntary autobiographical

    memories? *Memory & Cognition, 36,* 920–932.

    https://psycnet.apa.org/doi/10.3758/MC.36.5.920

Schlagman, S., Kliegel, M., Schulz, J., & Kvavilashvili, L. (2009). Differential effects of age on

    involuntary and voluntary autobiographical memory. *Psychology and Aging, 24*, 397–

    411. https://psycnet.apa.org/doi/10.1037/a0015785

Seli, P., O'Neill, K., Carriere, J. S., Smilek, D., Beaty, R. E., & Schacter, D. L. (2020). Mind-

    wandering across the age gap: Age-related differences in mind-wandering are partially

    attributable to age-related differences in motivation. *The Journals of Gerontology: Series*

    B. doi.org/10.1093/geronb/gbaa031

Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior

    parietal cortex to episodic memory. *Nature Reviews Neuroscience*, *18*(3), 183–192.

    https://doi.org/10.1038/nrn.2017.6

Sharps, M. J., & Antonelli, J. R. S. (1997). Visual and semantic support for paired-associates

    recall in young and older adults. *The Journal of Genetic Psychology, 158*(3), 347-355.

    https://doi.org/10.1080/00221329709596673

Strunk, J., & Duarte, A. (2019). Prestimulus and poststimulus oscillatory activity predicts

    successful episodic encoding for both young and older adults. *Neurobiology of Aging, 77*,

    1-12. https://doi.org/10.1016/j.neurobiolaging.2019.01.005

Toepper, M., Gebhardt, H., Bauer, E., Haberkamp, A., Beblo, T., Gallhofer, B., Driessen, M., &
Sammer, G. (2014). The impact of age on load-related dorsolateral prefrontal cortex
activation. *Frontiers in aging neuroscience*, *6*, 9. https://doi.org/10.3389/fnagi.2014.00009

Tschentscher, N., & Hauk, O. (2016). Frontal and parietal cortices show different spatiotemporal
dynamics across problem-solving stages. *Journal of cognitive neuroscience*, *28*(8), 1098–
1110. https://doi.org/10.1162/jocn_a_00960

van Noordt, S. J. R., White, L. O., Wu, J., Mayes, L. C., & Crowley, M. J. (2015). Social
exclusion modulates event-related frontal theta and tracks ostracism distress in children.
NeuroImage, 118, 248–255.
https://psycnet.apa.org/doi/10.1016/j.neuroimage.2015.05.085

Waldhauser, G., Johansson, M., & Hanslmayr, S. (2012). Brain oscillations indicate inhibition of
interfering visual memories. *Journal of Neuroscience, 32*, 1953–1961.
https://doi.org/10.1523/JNEUROSCI.4201-11.2012

Waldhauser, G. T., Braun, V., & Hanslmayr, S. (2016). Episodic memory retrieval functionally
relies on very rapid reactivation of sensory information. *The Journal of
Neuroscience*, *36*(1), 251–260. https://doi.org/10.1523/JNEUROSCI.2101-15.2016

Wang, T. H., de Chastelaine, M., Minton, B., & Rugg, M. D. (2012). Effects of age on the neural
correlates of familiarity as indexed by ERPs. *Journal of Cognitive Neuroscience, 24*(5),
1055–1068. https://doi.org/10.1162/jocn_a_00129

Wang, C., Rajagovindan, R., Han, S., Ding, M. (2016). Top-down control of visual alpha
oscillations: Sources of control signals and their mechanisms of action. *Frontiers in
Human Neuroscience, 10*, 15. https://doi.org/10.3389/fnhum.2016.00015

Woodruff, D. S., & Kramer, D. A. (1979). Eeg alpha slowing, refractory period, and reaction

time in aging. *Experimental Aging Research*, *5*(4), 279–292.

https://doi.org/10.1080/03610737908257205