

Neural correlates of auditory sensory memory dynamics in the aging brain



Sandeepa Sur^{a,b,*}, Edward J. Golob^{b,c,d}

^a Department of Radiology, Johns Hopkins University, Baltimore, MD

^b Program in Aging, Tulane University, New Orleans, LA

^c Department of Psychology, University of Texas, San Antonio, TX

^d Department of Psychology, Tulane University, New Orleans, LA

ARTICLE INFO

Article history:

Received 20 March 2019

Received in revised form 22 December 2019

Accepted 24 December 2019

Available online 30 December 2019

Keywords:

Mismatch negativity

MMN

Sensory memory

Repetition effects

Aging

ABSTRACT

The auditory system allows us to monitor background environmental sound patterns and recognize deviations that may indicate opportunities or threats. The mismatch negativity and P3a potentials have generators in the auditory and inferior frontal cortex and index expected sound patterns (standards) and any aberrations (deviants). The mismatch negativity and P3a waveforms show increased positivity for consecutive standards and deviants preceded by more standards. We hypothesized attenuated repetition effects in older participants, potentially because of differences in prefrontal functions. Young (23 ± 5 years) and older (75 ± 5 years) adults were tested in 2 oddball paradigms with pitch or location deviants. Significant repetition effects were observed in the young standard and deviant waveforms at multiple time windows. Except the earliest time window (30–100 ms), repetition effects were absent in the older group. Repetition effects were significant at frontal but not temporal lobe sites and did not differ among pitch and location deviants. However, P3a repetition was evident in both ages. Findings suggest age differences in the dynamic updating of sensory memory for background sound patterns.

Published by Elsevier Inc.

1. Introduction

Certain facets of attention control are thought to decline during normal cognitive aging (Kramer and Madden, 2008). Attention can be guided by either voluntary control, such as consciously deciding to eavesdrop on a nearby conversation, or automatically, as when a loud noise captures attention regardless of one's volition. Most attention models only distinguish between the controlled and automatic aspects of attention control. A recent model proposes a third category called “selection history,” where attention control is automatically guided by information in short-term and long-term memory (Addelman and Jiang, 2019; Awh et al., 2012; Theeuwes, 2019). The idea that attention can be guided by memory has a long heritage (James, 1890; Pillsbury, 1908). An example of a short-term influence on attention control is the lingering effects of recently attended information on current trial performance. Longer-term influences on attention control include the learned statistical properties, reward value, or personal significance of stimuli (Anderson, 2013; Moray, 1959; Theeuwes, 2019). Behavioral

studies show that aging is associated with decline in both controlled and automatic attention control (Escera et al., 2000; Hamm and Hasher, 1992). According to the framework of Awh et al., automatic attention control can be driven by salience (e.g., loudness of an unexpected sound), or selection history (e.g., stimulus patterns, probability, and priming).

Selection history includes aspects of implicit processing such as single stimulus or paired-stimuli repeats, which are thought to be well preserved in aging (Curran, 1997), whereas other implicit processes such as learning complex sequences show age decline (Bennett et al., 2006). Most of the repetition priming effects research includes investigation of retrieval strategies or response speed/accuracy (Howard and Howard, 2013; Ikier et al., 2008) and therefore does not examine the initial sensory encoding and memory. Recent studies in younger participants have suggested that auditory repetition effects observed during the initial auditory encoding might tap into the neural correlates of memory traces underlying priming (Aukstulewicz and Friston, 2016; Cooper et al., 2013; Friston et al., 2005). However, no prior studies have addressed whether early auditory encoding processes might underlie priming processes in cognitive aging.

Automatic neural responses can be studied in a passive listening “oddball” paradigm. In oddball paradigms, a repetitive

* Corresponding author at: Department of Radiology, Johns Hopkins University, Baltimore, MD 21287. Tel.: (+443) 904-4237; fax: 410-502-5133.

E-mail address: ssur3@jhmi.edu (S. Sur).

“standard” sound is intermittently punctuated by a “deviant” sound that differs from the standard in terms of a stimulus feature, such as pitch or location (Näätänen et al., 1978). Any attention capture by deviants, in this case, would be guided by saliency.

Neural responses in the oddball task are commonly measured with electroencephalogram (EEG), by averaging responses shortly before and after each stimulus (“event-related potentials” [ERPs]). Typically, the standard ERP is subtracted from the deviant ERP waveform. The resulting difference waveform is characterized by 2 prominent peaks: a negative peak, the “mismatch negativity” (MMN, ~100–250 ms latency), and a positive peak called the “P3a” (~250–280 ms latency). The MMN indexes change detection in the environment, such as a deviant sound (Alain et al., 1998; Halgren et al., 1995). The P3a reflects the orienting response and is larger for deviant stimuli that are more distinct from the standards in both passive and active tasks (Friedman et al., 2001; Wronka et al., 2008).

Selection history has a straightforward connection to ERP dynamics as a function of how many standards have been presented in a row between 2 deviant stimuli (termed “repetition effects”). Repetition effects are a well-known property of ERPs and indicate nonstationary brain responses (Golob et al., 2001; Golob and Starr, 2000). Repetition effects have been recorded at multiple spatial scales. Spatially, repetition effects capture auditory encoding as individual intracortical neuronal spiking in primates (Li et al., 1993; Miller and Desimone, 1994) and the summated neural activity of millions of neurons measured as blood-oxygen-level-dependent functional magnetic resonance imaging signal changes in humans (Grill-Spector et al., 2006).

In passive oddball paradigms, repetition effects in standard sounds are evident as increasing positivity at the time of the MMN, which is “reset” after presentation of a deviant (termed “repetition positivity” or “repetition suppression”) (Cooper et al., 2013; Haenschel et al., 2005). For deviant stimuli, the negative potential becomes more positive after longer sequences of standard stimuli (Costa-Faidella et al., 2011; Haenschel et al., 2005). Repetition effects are thought to index the development of a sensory memory trace, where the strength of these cortical representations in the auditory cortex increases with repeat number and is captured as a larger positivity in the standard waveform at the latencies of ~50–250 ms (Baldeweg et al., 2004; Cooper et al., 2013; Haenschel et al., 2005). Note that making grand average standard and deviant ERPs from all trials will obscure repetition effects.

We now turn from using the oddball task to index saliency and selection history to what is known about the cortical generators of standard and deviant ERP waves. Various studies suggest enhanced auditory cortex activity during MMN reflects prefrontal and temporoparietal cortical sources (lesion studies: Alain et al., 1998; Alho et al., 1994; animal studies: Javitt et al., 1994), where the prefrontal contributions to the MMN can be dissociated from auditory cortical activity (Deouell, 2007). A dissociation between frontal and temporal generators was initially provided by EEG current source density estimates of separate generators in the frontal and temporal cortex (Rinne et al., 2000), and intracranial recordings in humans (Halgren et al., 1995). A functional dissociation between these 2 generators was shown by selectively studying the reduction in frontal versus the temporal generator under various conditions (sleep: Sallinen and Lyytinen, 1997; schizophrenia: Alain et al., 1998; and alcohol: Jaaskelainen et al., 1996). Finally, interrelations between auditory and frontal MMN generators were supported by animal studies documenting reciprocal anatomical connections and short-latency single-unit responses to sounds in prefrontal regions (Azuma and Suzuki, 1984; Romanski et al., 1999). Similarly, the P3a has multiple generator sites in association cortex, including the prefrontal, anterior cingulate, and parietal areas (Halgren et al., 1998; Polich, 2007).

Separate temporal and frontal lobe generators of the MMN are relevant to aging because convergent evidence suggests that the prefrontal cortex undergoes substantial age-related structural changes at the cellular and regional levels (Raz, 1997; Sowell et al., 2003). Behavior studies of implicit sequence learning are germane to repetition effects, and white matter integrity of tracts to and from the dorsolateral prefrontal cortex is positively associated with sequence learning and negativity associated with age (Bennett et al., 2011). In contrast, sensory and motor cortices, including the primary and secondary auditory cortices, show little change with age (Flood and Coleman, 1988). Some prior studies found smaller MMN amplitudes and longer latencies in older (>~65 years) relative to younger (~20–30 years) participants (Cheng et al., 2013; Gaeta et al., 1998; Ruzzoli et al., 2012). However, other reports did not find significant age differences in MMN measures, particularly when sounds were delivered at a rapid rate and had obvious differences between standards and deviants (Cooray, 2014; Kiskey, 2005; Pekkonen et al., 1996). Studies investigating the P3a in passive oddball tasks generally report either longer latencies or smaller amplitudes in older participants (Friedman et al., 1998; Nowak et al., 2016).

The mixed results in aging may be due, in part, to methodological issues. Typically, MMN is expressed as a difference wave, which provides a convenient metric but also introduces 3 important ambiguities. First, a difference ERP waveform prevents analysis of the absolute voltage values and shapes of the constituent standard and deviant waveforms. Consequently, important age differences may go unrecognized if differences in one waveform are counteracted by the other waveform. It is noteworthy, however, that this did not happen in this data set. Second, difference measures generally have a lower signal-to-noise ratio, relative to single measures, because of contributions from 2 sources of variability (Cronbach and Furby, 1970). A smaller signal-to-noise ratio results in lower statistical power and test-retest reliability. Third, repetition effects are averaged out, which opens the possibility that age group differences may exist for the time course of repetition effects but not for grand averages.

We aim to test the prediction that MMN and P3a repetition effects for standards and deviants are evident in young adults but will be attenuated or absent in older participants. According to this hypothesis, the frontal cortex involvement may be important for stimulus selection history to influence auditory stimulus processing, and its influence would be expressed as repetition effects. Because age-related declines are more prominent in the frontal than auditory cortex, we predicted an absence or reduction of repetition effects in the older adults. Moreover, if repetition effects are less apparent in older participants, this may help explain some of the overall age differences observed in MMN and P3a measures when averaged across repetitions, as well as heterogeneity of findings across studies. Deviant stimuli were tested using 2 different stimulus dimensions (frequency, location), in separate blocks to check for generality and replicability of any age differences in repetition effects.

2. Methods

2.1. Participants

Twenty-seven young undergraduates (mean = 23 ± 5 years, M/F = 8/19) and 30 older community residents (mean = 75 ± 5 years, M/F = 11/19) were recruited. Older participants had no history of major neurological and psychiatric conditions and received a battery of standardized cognitive tests to screen for cognitive decline (see Golob et al., 2009). One participant with a low Mini-Mental State Examination score (MMSE = 20) was excluded. Hearing

thresholds were tested with an audiometer (Maico, Eden Prairie, MN), and all participants had thresholds <25 dB (0.5–4 kHz). Written informed consent was obtained from all participants for a protocol through the Tulane University IRB, and the experiments were consistent with the Declaration of Helsinki.

2.2. Study design

Two monaural pure tones (500 Hz and 1000 Hz; 100 ms duration; 10 ms rise/fall times, 80 dB SPL) were presented to either the left or right ear with an interstimulus interval (onset to onset) of 567 ms. Participants were instructed to watch a silent movie (“The Red Balloon”) and to ignore the sounds in the background. Spatial (monaural ear of presentation) and nonspatial (frequency) variables were chosen to tap into 2 major aspects of auditory processing. There were 4 stimulus blocks (1000 trials/block). Two blocks examined spatial deviants, where in each block, the same frequency tone was presented to one ear as the standard and the other as the deviant (ears counterbalanced across blocks) (Fig. 1). The other 2 blocks examined monaural pitch deviants using high- and low-frequency tones, and the standard/deviant frequencies were counterbalanced across blocks. The left and right ears for frequency deviants and frequencies for spatial deviants were approximately counterbalanced across participants. Stimuli were pseudorandomly presented to ensure adequate sampling of sequences and to avoid repetition of deviants. Stimulus probabilities were 0.945 for standards and 0.055 for deviants. Repetition effects examined runs of standards after a deviant (standard repetition effects) and numbers of standards before a deviant (for deviant repetition effects). To analyze standard ERP repetition effects, 4 positions within the run of standards after deviants were tested: 2, 6, 12, and 22 and 23 standards in a row. The numbers were chosen to approximately double, with 2 being the first opportunity for a repetition in the sequence. For deviant ERP repetition effects, trials were collapsed over a range of positions because there were far fewer trials versus the standards. The number of standards since the last deviant was examined for 9–12, 16–19, and 22 and 23. The grand average standard waveforms were obtained by averaging younger (71–82) and older (62–73) trials out of 108 total trials for repeat conditions 2, 6, and 12, and younger (43–45) and older (40) trials out of 60 total trials for repeat conditions 22 and 23. The grand average deviant waveforms were obtained by averaging (22–28) trials out of 30 deviant trials in both younger and older participants. EEG was recorded from 64-channel electrode caps using standard methods (Compumedics Neuroscan, Charlotte, NC, USA) (500 Hz sample rate, direct current-100 Hz bandpass, was visually inspected for artifacts). The reference during recording was placed between Cz and CPz and re-referenced offline to the

average reference (see Mock et al., 2015). Offline band-pass filtering (0.1, 30 Hz) of the waveforms was performed. Baseline was performed from -100 to 0 ms. EEG was corrected for direct current drift and eye blink artifacts in Neuroscan using an algorithm (Gratton et al., 1983). ERPs to stimuli were averaged from EEG sweeps between -100 ms to 400 ms relative to stimulus onset.

2.3. Statistical analysis

Prior research informed the selection of frontal (10/20 system, Fz) and temporal (M1, M2) electrode sites to measure the repetition effects in different temporal windows and MMN and P3a. Mean voltage (ERP amplitude) was quantified for each of the time windows as a function of repetition effect (Friedman et al., 2001; Näätänen et al., 2007). Analysis of standards used three time windows (30–100 ms, 90–130 ms, and 132–200 ms), which were common to both age groups. This common window approach was necessary to account for the latency differences between the ERP peaks for each age group. Additional analysis was performed for time windows that best captured these peaks in each age group, where age-specific nonoverlapping time windows were used to capture the age-appropriate window latencies, regardless of length, or trying to make the windows comparable for analysis. The 2 new standard windows were 50–98 ms and 100–130 ms in the younger participants and 30–78 and 80–130 ms in the older participants.

Deviant waveforms are shown in Fig. 2B, with 2 time window measures (90–130 ms MMN and 200–260 ms P3a). Separate analysis of variance tests (ANOVAs, significance = $p < 0.05$) were performed for each time window, using the factors of age (younger vs. older), stimulus type (frequency vs. location), and repetition ((standards: 2, 6, 12, 22, and 23); deviants: (9–12), (16–19), and (22–24)). Planned contrasts were used for post hoc analyses involving the factor of repetition.

Repetition effects in this study were compared with previous MMN studies through the classical MMN measure, obtained by subtracting standards from deviants (90–130 ms window). The 12 and 22 repetition points were common to both standards and deviants. Note that in deviants, 9–12 repetitions and 22–24 repetitions were summated in an ERP average because of fewer numbers of trials. These trial summations were performed to ensure that each condition had at least 60 trials or more per condition.

3. Results

3.1. Standard tones at frontal site (Fz)

ERPs and plots of amplitudes in each time window for standard tones are presented in Fig. 2. Analysis of frontal activity used 2 (age) \times 2 (stimulus type) \times repetition position (4) ANOVAs, with separate analyses at 3 time windows that corresponded to peaks of the waveforms (Fig. 2A). The 30–100 ms window showed a main effect of age ($F_{(1, 55)} = 24.6, p < 0.001$) and a significant age \times repetition interaction ($F_{(3, 165)} = 24.6, p < 0.001$). The main effect was due to more positive amplitudes in the young group. Follow-up quadratic contrasts examined the age \times repetition interaction and found significant effects in both age groups (both p 's < 0.05) (Fig. 2, lower left panel). Repetition effects in young participants were manifest as progressive amplitude increase across repetition lengths of 2, 6, 12 standards in a row, which then plateaued or had a slight decrease between 12 and 22 and 23 repetitions. In contrast, amplitudes in older participants across 2, 6, and 12 repetitions were comparable, and only showed an amplitude increase for the longest repetition tested (22 and 23 standards in a row). Thus, the onset of repetition effects in the older adults was greatly delayed relative to

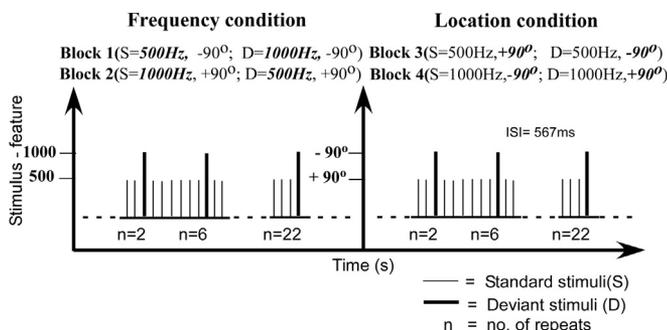


Fig. 1. Schematic illustration of stimulus sequence structure.

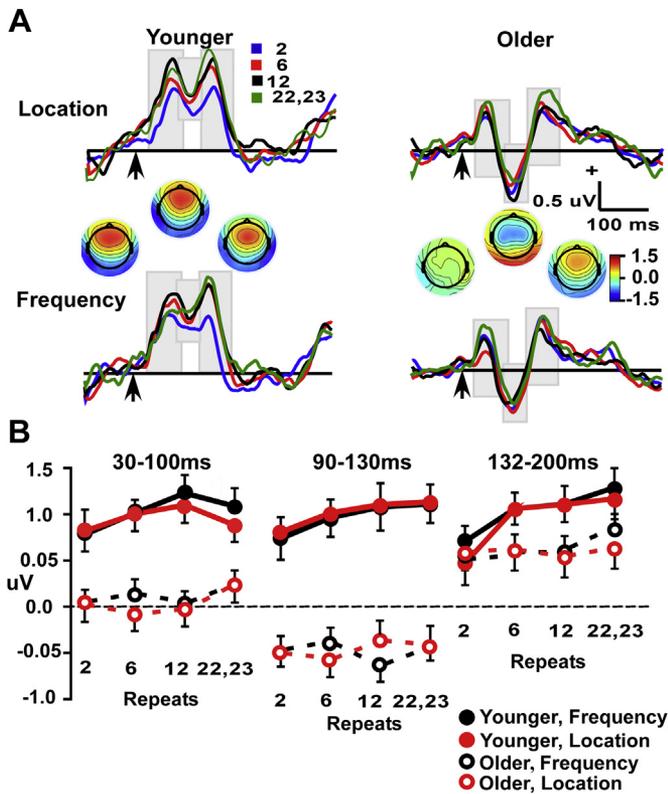


Fig. 2. (A) Standard frontal repetition effects (at Fz electrode) in location and frequency waveforms across 3 windows (30–100 ms, 90–130 ms, and 132–200 ms), for younger (left) and older (right) participants. The arrow indicates stimulus onset. (B). Line plots demonstrate the repetition effect in aging across 4 repeat conditions (2, 6, 12, and 22–23) in 3 time windows (30–100 ms, 90–130 ms, and 132–200 ms).

the younger adults. There was no main effect or interaction involving the stimulus type factor.

The 132–200 ms window showed a significant main effect of repetition ($F_{(3, 165)} = 7.4, p < 0.001$) that was qualified by age \times repetition interaction ($F_{(3, 165)} = 3.6, p < 0.02$). Planned contrasts showed a significant linear fit in the young ($p < 0.001$) but not in older participants ($p > 0.25$). As with the 30–100 ms window analysis, there were no significant differences among stimulus types, which indicate some generality to the findings. The same analysis was conducted with window measures more specific to each age group, and the same results were found (see [Supplementary Methods](#)). The 90–130 ms window showed a significant age effect ($F_{(1, 55)} = 39.3, p < 0.001$), with more positive amplitudes in the young group.

3.2. Standard tones at mastoid sites (M1, M2)

Analysis of the mastoid sites used 2 (age) \times 2 (stimulus type) \times repetition position (4) \times 3 (time window) \times 2 (site: M1, M2) ANOVAs. As seen in [Fig. 3](#), the 30–100 ms window showed significant effects for age ($F_{(1, 55)} = 17.5, p < 0.001$). The effect for site was significant in this window ($F_{(1, 55)} = 8.1, p < 0.01$) (not shown in [Fig. 3](#)), with more negative potentials in the young versus older and left versus right mastoids. The only significant effect for the 90–130 ms window was that of age ($F_{(1, 55)} = 41.4, p < 0.001$, with young more positive than older). In the 132–200 ms window, there was a small effect of electrode site ($F_{(1, 55)} = 4.1, p < 0.05$), with more negative potentials at the right site (M2) (not shown in the [Fig. 3](#)). Overall, the absence of repetition effects to standard tones at

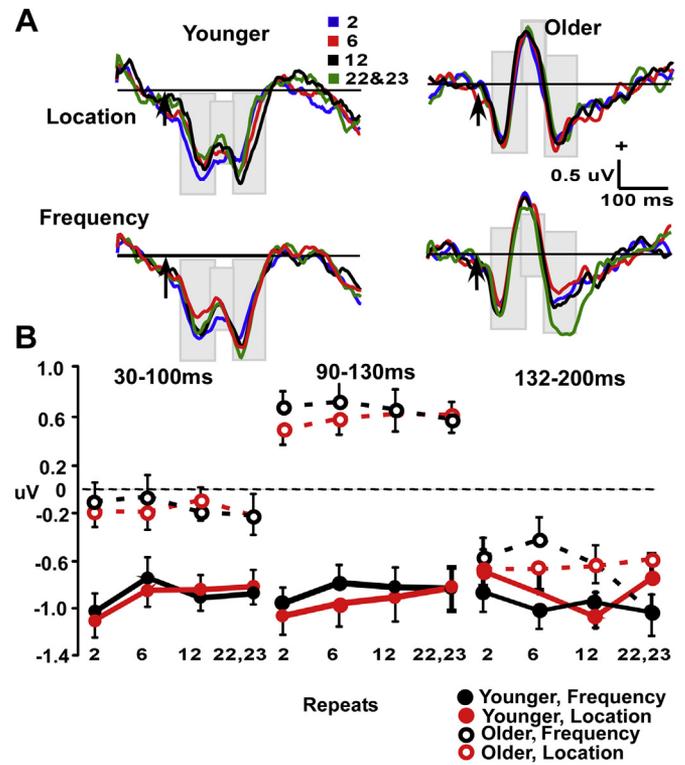


Fig. 3. (A) Standard temporal repetition effects (combined left and right Mastoid electrode sites) in location and frequency waveforms across 3 windows (30–100 ms, 90–130 ms, and 132–200 ms), for younger (left) and older (right) participants. The arrow indicates stimulus onset. (B). Line plots demonstrate the repetition effect in aging across 4 repeat conditions (2, 6, 12, and 22–23) in 3 time windows (30–100 ms, 90–130 ms, and 132–200 ms).

mastoid sites contrasts with the age differences in repetition effects seen at the frontal site.

3.3. Deviant tones at frontal site (Fz)

Plots of the results for deviant stimuli are shown in [Fig. 4](#). Recall that the 90–130 ms window indexes the MMN, whereas the 200–260 window captures the P3a peak. Analysis of frontal activity between 90 and 130 ms using a 2 (age) \times 2 (stimulus type) \times repetition position (3) \times 2 (time window) ANOVA had significant effects of age ($F_{(1, 55)} = 16.2, p < 0.001$) and an age \times repetition interaction ($F_{(2, 110)} = 8.5, p < 0.05$). The age effect was due to larger, more negative, amplitudes in older versus younger participants. Contrasts to better understand the age \times repetition interaction showed a linear fit over repetitions in the young ($p < 0.001$), which was not evident in older participants ($p = 0.22$). For the 200–260 ms window, there was an effect of age ($F_{(1, 55)} = 28.6, p < 0.001$), with larger P3a amplitudes in the young.

3.4. Deviant tones at mastoid sites (M1, M2)

As seen in [Fig. 5](#), in the MMN (90–130 ms) time window, there was only a significant effect of age ($F_{(1, 55)} = 12.9, p < 0.001$) due to more positive potentials in the young participants. For the P3a (200–260 ms) window, there were main effects of age ($F_{(1, 55)} = 8.7, p < 0.01$) and site ($F_{(1, 55)} = 14.7, p < 0.001$), with more positive potentials in the young versus older and for the right versus left mastoid site. There was also a significant age \times stimulus type interaction ($F_{(1, 55)} = 6.5, p < 0.02$) because age differences were larger for the location versus frequency deviants.

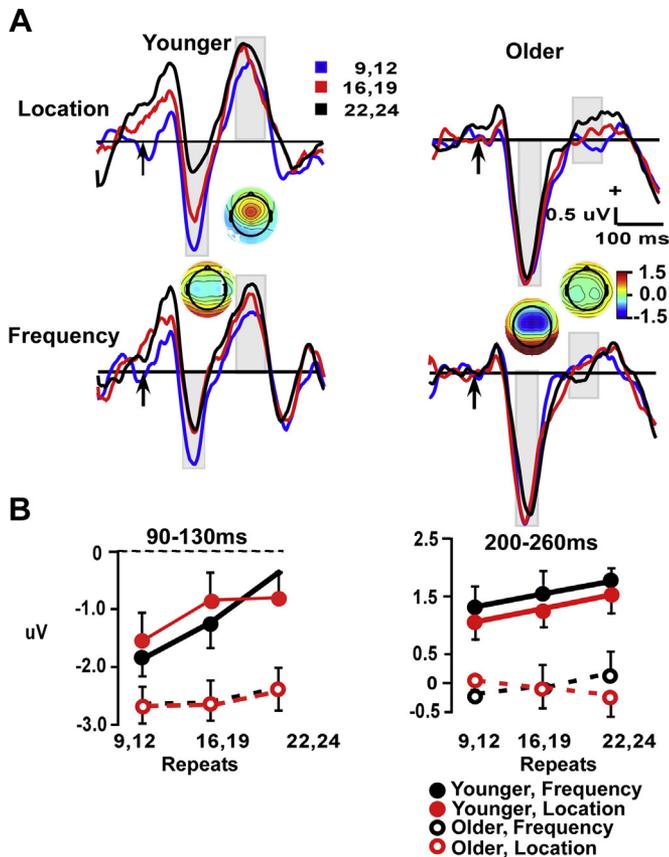


Fig. 4. (A) Deviant frontal repetition effects (at Fz electrode site) in location and frequency waveforms across 90–130 ms and 200–260 ms, P3a windows, in younger (left) and older (right) participants. The arrow indicates stimulus onset. (B) Line plots demonstrate the repetition effect in aging across 3 repeat conditions (9–12, 16–19, and 22–24) in 2 time windows (90–130 ms and 200–260 ms).

3.5. Subtraction waveform (deviant minus standard) at frontal site (Fz)

Because repetition effects were only observed at the frontal site for standards and deviants, they are presented in this article as subtraction waveforms at just the frontal site to isolate the MMN (90–130 ms) and P3a (200–260 ms) (Fig. 6). Limited number of trials was available for the infrequent deviants to create ERP averages. Therefore, repetition effects were measured after 12 and 22 standards in a row, the 2 repetition points common to both standards and deviants. For the MMN measure, a 2 (age) \times 2 (stimulus type) \times repetition position (2) ANOVA had a main effect of repetition ($F_{(1, 55)} = 10.8, p < 0.01$) and an age \times repetition interaction ($F_{(1, 55)} = 5.3, p < 0.03$). As seen in Fig. 6, the interaction was driven by a significant repetition effect in the young ($p < 0.01$), which was absent in the older participants ($p < 0.42$). There was no significant overall effect of age ($p < 0.51$).

For the P3a measure, there was a main effect of age ($F_{(1, 55)} = 63.82, p < 0.001$: young > older), a trend for a repetition effect ($F_{(1, 55)} = 3.21, p = 0.075$), and a significant repetition \times stimulus type interaction ($F_{(1, 55)} = 4.11, p < 0.05$). The age \times repetition \times feature was not significant ($p = 0.87$). The interaction between repetition and stimulus type was significant because of repetition effects in the frequency but not location condition, and is similar to earlier findings that show significant repetition at the same location (Leung et al., 2013).

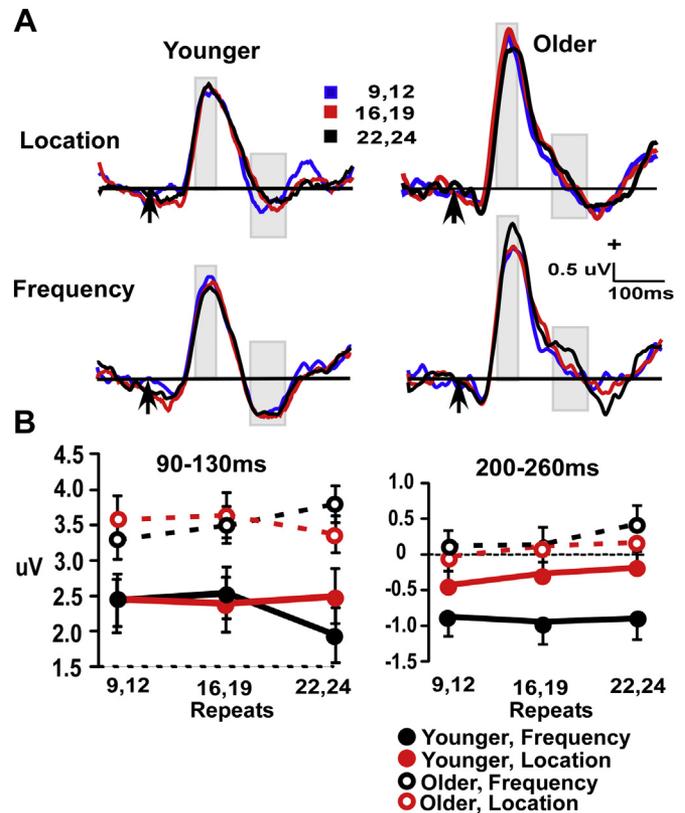


Fig. 5. (A) Deviant temporal repetition effects (combined left and right mastoid electrode sites) in location and frequency waveforms across 90–130 ms and 200–260 ms, P3a windows, in younger (left) and older (right) participants. The arrow indicates stimulus onset. (B) Line plots demonstrate the repetition effect in aging across 3 repeat conditions (9–12, 16–19, and 22–24) in 2 time windows (90–130 ms and 200–260 ms).

See [Supplementary Fig. 1](#) for analysis of repetition effects in MMN at the temporal sites, which generally did not yield significant findings.

4. Discussion

The main results demonstrated that the standard and deviant waveforms in the young had significant repetition effects in multiple time windows at frontal but not temporal sites. In contrast, with one exception (standards: 30–100 ms), older participants did not have repetition effects. These findings indicate age differences in the degree to which the selection history influences the processing of incoming stimuli, with the young adults having a much greater influence of selection history. Age differences were significant for repetition effects regardless of the sensory feature used to define the deviant sound (frequency vs. location), which indicates some generality of the age differences. Similarly, the subtraction waveform (deviants minus standards) also only had significant MMN repetition effects in younger participants, whereas P3a repetition effects were seen in both age groups. Taken together, these findings provide new evidence of dynamic adjustment in processing of standard and deviant sounds in young but not older adults. The absence of such dynamics in older participants, in tandem with the large literature on generators of the MMN, suggests a fruitful new approach to understanding specific neural mechanisms for age differences in sensory memory and attention control.

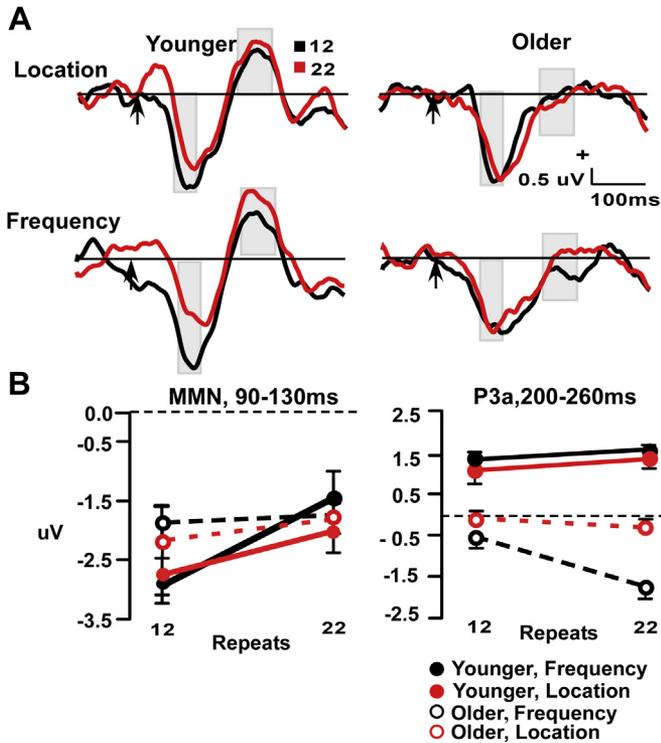


Fig. 6. (A) Difference waveform frontal repetition effects (deviant minus standard) waveforms at electrode site Fz. Time windows index the MMN (90–130 ms) and P3a (200–260 ms). The arrow indicates stimulus onset. (B) Line plots demonstrate repetition effect in aging across 2 repeat conditions, 12 and 22 in 2 time windows (90–130 ms and 200–260 ms).

4.1. Age differences in repetition effects for standards and deviants

Prior studies using passive oddball or roving paradigms, where standards and deviants vary over time, have consistently observed repetition effects to standards at frontal electrode sites in the young (Baldeweg et al., 2004; Haenschel et al., 2005; Horvath et al., 2008; Nowak et al., 2016). Repetition effects were observed at temporal sites in a study where participants actively discriminated among stimuli (Haenschel et al., 2005). According to the “repetition suppression” account, repetition effects seen in the standard waveform reflect auditory sensory memory trace formation (Cooper et al., 2013; Haenschel et al., 2005). However, because most repetition effect studies, including the present one, use passive listening, the often-hypothesized relationship between echoic memory, as defined by behavioral measures, and ERP repetition effects is currently uncertain.

We propose that sequence effects reflect attention guidance by selection history because there was no behavioral goal (participants passively listened to the sounds), and the same physical stimuli were presented across sequences, so there were no sequence differences in stimulus saliency. Although most measures of standard and deviant ERPs showed repetition effects in young participants, there were generally no significant repetition effects in the older participants. The one exception was in the earliest time window for standards (30–100 ms), where repetition effects were observed in the older participants, but only after many (22 or 23) standards in a row. At this point, repetition effects were first evident in the older participants; and repetition effects in the young group had stopped.

The present findings suggest a distinction between sensory memory driving the presence of an MMN/P3a potential and dynamic updating of these and other potentials over trials. When the

MMN was calculated using standard methods by averaging across all trials and subtracting deviants from standards, the overall MMN amplitude was about the same in both age groups. Thus, the general lack of repetition effects in the older group is not due to an inability to generate robust potentials. Rather, age differences in repetition effects seem to be specific to the dynamic updating and maintenance of MMN-related representations across trials (review, Irvine, 2018). Prior work showing age differences in MMN amplitude elicited by patterns across trials may also be relevant to selection history (Alain et al., 1999).

Auditory ERP repetition effects have been corroborated by several magnetoencephalography studies (Todorovic et al., 2011; Aine et al., 2005); functional magnetic resonance imaging: (Grady et al., 2011), and some report age differences in neural adaptation (Grady et al., 2011; Leung et al., 2013). Repetition effects and normal aging have been explored in task-based priming experiments using 3 or 4 repetitions (Aine et al., 2005; Grady et al., 2011), or in passive listening tasks with 2 (Golob et al., 2001) or 4 (Leung et al., 2013) stimuli in a row. The present study focused on delineating the effects of longer repeats on automatic attention control mechanisms, with a wide range of repetition lengths.

To have a sufficient number of trials for deviant averages, sequence effects were not measured for each possible sequence position. Standards were measured after 2 standards in a row after a deviant, then 6, which then doubled to 12 and then nearly doubled again to 22 or 23 standards in a row. Future work would be needed to map in between the measured sequences here and to determine if repetition effects are present in older participants for sequences longer than 22 or 23 standards. Note that earlier studies have reported age-related attenuation in amplitudes for N100 and P200 sensory potentials (Anderer et al., 1996), which have been thought to indicate age-related inhibitory decline (Boutros et al., 2000). Prior studies have shown attenuated N1 and P2 amplitudes after stimulus repetition, which are thought to indicate impaired inhibitory control (Boutros, 2000; Fuerst et al., 2007; Näätänen and Picton, 1987).

Repetition effects at the midline frontal site to deviants have been observed in a passive oddball condition (Heinemann et al., 2011), but there have been mixed findings under passive roving conditions (Recasens et al., 2015 vs. Haenschel et al., 2005; Cooper et al., 2013; Baldeweg et al., 2004). Cooper et al. (2013) did not find repetition effects in deviants using sequences up to 16 repeats. In contrast, a study with a similar design except that repeat lengths ranged from 16 to 36 did find significant repetition effect in the deviants (Baldeweg et al., 2004), suggesting that perhaps a minimum number of repeats were needed. Despite the fact that there is no satisfactory explanation for Cooper’s findings, one could summarize that the absence of repetition in deviants during a passive roving task could be attributed to (1) the fast turnover of the deviant features, and the cumulative effect of deviation in several features during a roving condition or (2) the need for a minimum length of stimulus repeats preceding the deviant to extract repetition effects.

4.2. Age differences in repetition effects for subtraction waveforms (MMN, P3a)

The MMN repetition effects were significant in the younger participants in this study and corroborate earlier study findings (Costa-Faidella, 2011; Haenschel et al., 2005; Horvath et al., 2008; Nowak et al., 2016). As with the separate measures of standard and deviant ERPs, MMN repetition effects were absent in older participants. In contrast, P3a repetition effects were observed in both age groups for the frequency domain. Note that repetition effects were not present in either group when analyzing the deviants, which are classically thought to elicit the P3a (Friedman

et al., 2001). Nonetheless, in the subtraction waveform, there were significant repetition effects reflecting the contrast between standard and deviant stimulus processing, at least from 100–130 ms.

Although it is counterintuitive, we speculate that the strength of sensory memory, as indicated by the MMN, might initially be stronger but static over trials in older participants. In younger adults, sensory memory may strengthen and then exceed the level of older participants after enough repetitions. This would explain why there were no overall differences in MMN amplitude. It is possible that strengthening of memory traces during repetition suppression in the standards (young & old), and repetition enhancement in the deviants (young only), might also contribute to lowering the threshold for attention capture (P3a repetition effects) in young versus older participants.

The lack of age differences in overall MMN amplitude is consistent with other reports (review by Cooray, 2014; Kisley, 2005), yet other studies have observed smaller MMN amplitudes and longer latencies in older versus younger adults (Cheng et al., 2013; Gaeta et al., 1998; Ruzzoli et al., 2012). The mixed age-related findings in MMN are likely due to a wide variety of experimental designs, analysis techniques (Peter et al., 2010; Jacobsen and Schröger, 2003), and methods to control for age-related hearing deficits. Finding comparable overall MMN amplitudes in young and older adults seems to be most likely when the sounds are delivered rapidly, and there are obvious differences in stimulus features, such as pitches differing by an octave or far left/right locations, among standards and deviants.

It is worth noting that although the MMN measured from the subtraction waveform had no overall age differences here, there were large amplitude differences among age groups when the standard and deviant ERPs were examined separately. Hence, examining standard and deviant waveforms separately may help better understand any mixed results regarding age effects in subtraction waveforms.

The P3a follows the MMN in passive oddball paradigms. In the present study, the pattern of results was opposite to the MMN. Although there was an overall age difference for the P3a amplitude and a modest trend for a repetition effect, these factors did not significantly interact. These age differences in overall P3a amplitude have been interpreted to reflect age-related reduction in the automatic orientation of attention (Nowak et al., 2016; Walhovd and Fjell, 2001). On the one hand, these results favor potential differences in automatic orienting, as the standard and deviant tones were readily distinguishable by pitch (one octave) and location (left or right ears). On the other hand, the age-related preservation of repetition suppression and enhancement effects in the older participants suggest that repetition effects might be influencing attention capture and need to be tested further.

The repetition effects in the MMN are termed, “MMN memory trace effects” and are related to auditory sensory memory trace formation (Baldeweg et al., 2004). The MMN has classically been interpreted as indexing a comparison between the current stimulus and a memory template of recent stimuli (Alain et al., 1998; Näätänen et al., 2005). More recently, within the predictive coding framework, the MMN has been proposed to not only index recent sensory experience but also engender a prediction about upcoming stimuli (Friston, 2005). The absence of MMN repetition effects in older participants suggests a crucial role of the frontal cortex in mediating the repetition effects through selection history, during information processing after encoding, which further suggests building a context for the incoming background sounds. This assertion could be tested in future work by using the absent MMN repetition effects in the older group to distinguish template versus predictive coding models for MMN and P3a functions (Carbajal and Malmierca, 2018; Schröger et al., 2015).

Recent studies of macaque cortical activity show that ascending and descending neural tracts might have different spectral information. For example, synchronization between cortical areas within the gamma band was related to ascending connections from hierarchically lower (sensory) to higher (frontal) regions (Bosman et al., 2012), whereas descending connections were related to interareal synchronization in the beta band (Bastos et al., 2015). Further exploration could elucidate midlatency components (~10–50 ms), which were not directly observed in the ERP measures (see review Grimm et al., 2016), and other oscillatory components such as theta (Hsiao et al., 2009) or gamma band network dynamics (Nicol et al., 2011), particularly to examine interactions between auditory and prefrontal cortical generators. This would help clarify the exact timing of involvement of various regions in auditory information processing and selection history, which remains a bit vague as of now.

5. Conclusions

In summary, the findings support the idea that automatic auditory processing that is guided by selection history is largely absent in the older participants. We speculate that this might be due to age differences in the interplay of auditory and inferior prefrontal circuits thought to generate the MMN and related responses. Our results from separately examining repetition effects in standards and deviants, along with the classical MMN/P3a difference wave, show that subtraction can obscure cortical dynamics underlying age differences. We suggest that repetition effects and their temporal dynamics not only explain some of the mixed results in aging and MMN/P3a but also provide a noninvasive way to examine neural correlates of auditory sensory memory in the aging brain. The observed dynamics can be used in the future as a noninvasive way to probe interactions between sensory and association cortices, and to examine the functional implications of networks between regions with large age-related decline and their interactions with areas with little morphological differences during normal aging.

Disclosure statement

The authors report no conflict of interest.

CRediT authorship contribution statement

Sandeepa Sur: Conceptualization, Methodology, Software, Data curation, Writing - original draft, Visualization, Investigation.
Edward J. Golob: Supervision, Validation, Writing - original draft.

Acknowledgements

This research was supported by NIH grants P20GM103629 and R01DC014736.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neurobiolaging.2019.12.020>.

References

- Ardleman, D.A., Jiang, Y.V., 2019. The influence of selection history on auditory spatial attention. *J. Exp. Psychol. Hum. Percept. Perform.* 45, 474–488.
- Alain, C., Woods, D.L., Knight, R.T., 1998. A distributed cortical network for auditory sensory memory in humans. *Brain Res.* 812, 23–37.

- Aine, C.J., Adair, J.C., Knoefel, J.E., Hudson, D., Qualls, C., Kovacevic, S., Woodruff, C.C., Cobb, W., Padilla, D., Lee, R.R., Stephen, J.M., 2005. Temporal dynamics of age-related differences in auditory incidental verbal learning. *Cogn. Brain Res.* 24, 1–18.
- Alain, C., Hargrave, R., Woods, D.L., 1998a. Processing of auditory stimuli during visual attention in patients with schizophrenia. *Biol. Psychiatry* 44, 1151–1159.
- Alain, C., Cortese, F., Picton, T.W., 1999. Event-related brain activity associated with auditory pattern processing. *Neuroreport* 10, 2429–2434.
- Alho, K., Woods, D.L., Algazi, A., Knight, R.T., Näätänen, R., 1994. Lesions of frontal cortex diminish the auditory mismatch negativity. *Electroencephalogr. Clin. Neurophysiol.* 91, 353–362.
- Anderer, P., Semlitsch, H.V., Saletu, B., 1996. Multichannel auditory event-related brain potentials: effects of normal aging on the scalp distribution of N1, P2, N2 and P300 latencies and amplitudes. *Electroencephalogr. Clin. Neurophysiol.* 99, 458–472.
- Anderson, B.A., 2013. A value-driven mechanism of attentional selection. *J. Vis.* 13, 7.
- Auksztulewicz, R., Friston, K., 2016. Repetition suppression and its contextual determinants in predictive coding. *Cortex* 80, 125–140.
- Awh, E., Belopolsky, A.V., Theeuwes, J., 2012. Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn. Sci.* 16, 437–443.
- Azuma, M., Suzuki, H., 1984. Properties and distribution of auditory neurons in the dorsolateral prefrontal cortex of the alert monkey. *Brain Res.* 298, 343–346.
- Baldeweg, T., Klugman, A., Gruzelić, J., Hirsch, S.R., 2004. Mismatch negativity potentials and cognitive impairment in schizophrenia. *Schizophr. Res.* 69, 203–217.
- Bastos, A.M., Vezoli, J., Bosman, C.A., Schoffelen, J.M., Oostenveld, R., Dowdall, J.R., DeWeerd, P., Kennedy, H., Fries, P., 2015. Visual areas exert feedforward and feedback influences through distinct frequency channels. *Neuron* 85, 390–401.
- Bennett, I.J., Golob, E.J., Parker, E.S., Starr, A., 2006. Memory evaluation in mild cognitive impairment using Recall and Recognition tests. *J. Clin. Exp. Neuropsychol.* 28, 1408–1422.
- Bennett, I.J., Madden, D.J., Vaidya, C.J., Howard, J.H., Howard, D.V., 2011. White matter integrity correlates of implicit sequence learning in healthy aging. *NBA* 32, 2317 e1–2317.e12.
- Bosman, C.A., Schoffelen, J.M., Brunet, N., Oostenveld, R., Bastos, A.M., Womelsdorf, T., Rubehn, B., Stieglitz, T., De Weerd, P., Fries, P., 2012. Attentional stimulus selection through selective synchronization between monkey visual areas. *Neuron* 75, 875–888.
- Boutros, N.N., Carrington, R.M., Petrakis, I., Campbell, D., Torello, M., Krystal, J., 2000. Similarities in the disturbances in cortical information processing in alcoholism and aging: a pilot evoked potential study. *Int. Psychogeriatr.* 12, 513–525.
- Carbajal, G.V., Malmierca, M.S., 2018. The neuronal basis of predictive coding along the auditory pathway: from the subcortical roots to cortical deviance detection. *Trends Hear.* 22, 1–33.
- Cheng, C.H., Hsu, W.Y., Lin, Y.Y., 2013. Effects of physiological aging on mismatch negativity: a meta-analysis. *Int. J. Psychophysiol.* 90, 165–171.
- Cooper, R.J., Atkinson, R.J., Clark, R.A., Michie, P.T., 2013. Event-related potentials reveal modelling of auditory repetition in the brain. *Int. J. Psychophysiol.* 88, 74–81.
- Cooray, G., Garrido, M.I., Hyllienmark, L., Brismar, T., 2014. A mechanistic model of mismatch negativity in the ageing brain. *Clin. Neurophysiol.* 125, 1774–1782.
- Costa-Faidella, J., Baldeweg, T., Grimm, S., Escera, C., 2011. Interactions between “what” and “when” in the auditory system: temporal predictability enhances repetition suppression. *J. Neurosci.* 31, 18590–18597.
- Cronbach, L.J., Furby, L., 1970. How we should measure “change”- or should we? *Psychol. Bull.* 74, 68–80.
- Curran, T., 1997. Effects Aging Implicit Sequence Learning: Account. *Seq. Struct. explicit knowledge.* *Psychol. Res.* 60, 24–41.
- Deouell, L.Y., 2007. The frontal generator of the mismatch negativity revisited. *J. Psychophysiol.* 21, 188–203.
- Escera, C., Alho, K., Schröger, E., Winkler, I.W., 2000. Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiol. Neurotol.* 5, 151–166.
- Flood, D.G., Coleman, P.D., 1988. Neuron numbers and sizes in aging brain: comparisons of human, monkey, and rodent data. *Neurobiol. Aging* 9, 453–463.
- Friedman, D., Cycowicz, Y.M., Gaeta, H., 2001. The novelty P3: an event-related brain potential (ERP) sign of the brain’s evaluation of novelty. *Neurosci. Biobehav. Rev.* 25, 355–373.
- Friedman, D., Kazmerski, V.A., Cycowicz, Y.M., 1998. Effects of aging on the novelty P3 during attend and ignore oddball tasks. *Psychophysiology* 35, 508–520.
- Friston, K., 2005. A theory of cortical responses. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 815–836.
- Fuerst, D.R., Gallinat, J., Boutros, N.N., 2007. Range of sensory gating values and test–retest reliability in normal subjects. *Psychophysiology* 44, 620–626.
- Gaeta, H., Friedman, D., Ritter, W., Cheng, J., 1998. An event-related potential study of age-related changes in sensitivity to stimulus deviance. *Neurobiol. Aging* 19, 447–459.
- Golob, E., Starr, A., 2000. Effects of stimulus sequence on event-related potentials and reaction time during target detection in Alzheimer’s disease. *Clin. Neurophysiol.* 111, 1438–1449.
- Golob, E.J., Miranda, G.C., Johnson, J.K., Starr, A., 2001. Sensory cortical interactions in aging, mild cognitive impairment, and Alzheimer’s disease. *Neurobiol. Aging* 22, 755–763.
- Golob, E.J., Medina, L.D., Bright, S., Ringman, J.M., Starr, A., Schaffer, B., Irimajiri, R., 2009. Cortical event-related potentials in preclinical familial Alzheimer disease. *Neurology* 73, 1649–1655.
- Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484.
- Grady, C.L., Charlton, R., He, Y., Alain, C., 2011. Age differences in fMRI adaptation for sound identity and location. *Front. Hum. Neurosci.* 5, 24.
- Grimm, S., Escera, C., Nelken, I., 2016. Early indices of deviance detection in humans and animal models. *Biol. Psychol.* 116, 23–27.
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10, 14–23.
- Haenschel, C., Vernon, D.J., Dwivedi, P., Gruzelić, J.H., Baldeweg, T., 2005. Event-related brain potential correlates of human auditory sensory memory-trace formation. *J. Neurosci.* 25, 10494–10501.
- Halgren, E., Baudena, P., Clarke, J.M., Heit, G., Liégeois, C., Chauvel, P., Musolino, A., 1995. Intracerebral potentials to rare target and distractor auditory and visual stimuli. I. Superior temporal plane and parietal lobe. *Electroencephalogr. Clin. Neurophysiol.* 94, 191–220.
- Halgren, E., Marinkovic, K., Chauvel, P., 1998. Generators of the late cognitive potentials in auditory and visual oddball tasks. *Electroencephalogr. Clin. Neurophysiol.* 106, 156–164.
- Hamm, V.P., Hasher, L., 1992. Age and the availability of inferences. *Psychol. Aging* 7, 56–64.
- Heinemann, L.V., Kaiser, J., Altmann, C.F., 2011. Auditory repetition enhancement at short interstimulus intervals for frequency-modulated tones. *Brain Res.* 1411, 65–75.
- Horváth, J., Winkler, I., Bendixen, A., 2008. Do N1/MMN, P3a, and RON form a strongly coupled chain reflecting the three stages of auditory distraction? *Biol. Psychol.* 79, 139–147.
- Howard, J.H., Howard, D.V., 2013. Aging mind and brain: is implicit learning spared in healthy aging? *Front. Psychol.* 4, 1–6.
- Hsiao, F.-J., Wu, Z.A., Ho, L.-T., Lin, Y.-Y., 2009. Theta oscillation during auditory change detection: a MEG study. *Biol. Psychol.* 81, 58–66.
- Ikier, S., Yang, L., Hasher, L., 2008. Implicit proactive interference, age, and automatic versus controlled retrieval strategies. *Psychol. Sci.* 19, 456–461. <http://doi.org/10.1111/j.1467-9280.2008.02109.x>
- Irvine, D.R., 2018. Plasticity in the auditory system. *Hear. Res.* 362, 61–73.
- Jääskeläinen, I.P., Pekkonen, E., Hirvonen, J., Sillanauke, P., Näätänen, R., 1996. Mismatch negativity subcomponents and ethyl alcohol. *Biol. Psychol.* 43, 13–25.
- Jacobsen, T., Schröger, E., 2003. Measuring duration mismatch negativity. *Clin. Neurophysiol.* 114, 1133–1143.
- James, W., 1890. *Attention. The principles of psychology*, 1, pp. 402–458.
- Javit, D.C., Steinschneider, M., Schroeder, C.E., Vaughan Jr., H.G., Arezzo, J.C., 1994. Detection of stimulus deviance within primate primary auditory cortex: intracortical mechanisms of mismatch negativity (MMN) generation. *Brain Res.* 667, 192–200.
- Kisley, M.A., Davalos, D.B., Engleman, L.L., Guinther, P.M., Davis, H.P., 2005. Age-related change in neural processing of time-dependent stimulus features. *Cogn. Brain Res.* 25, 913–925.
- Kramer, A.F., Madden, D.J., 2008. Chapter 5: attention. In: Craik, F.I.M., Salthouse, T.A. (Eds.), *The Handbook of Aging and Cognition*, third ed. Taylor & Francis, New York, NY, pp. 189–249.
- Leung, A.W.S., He, Y., Grady, C.L., Alain, C., 2013. Age differences in the neuroelectric adaptation to meaningful sounds. *PLoS One* 8, e68892.
- Li, L., Miller, E.K., Desimone, R., 1993. The representation of stimulus familiarity in anterior inferior temporal cortex. *J. Neurophysiol.* 69, 1918–1929.
- Miller, E.K., Desimone, R., 1994. Parallel neuronal mechanisms for short-term memory. *Science* 263, 520–522.
- Mock, J.R., Foundas, A.L., Golob, E.J., 2015. Speech preparation in adults with persistent developmental stuttering. *Brain Lang.* 149, 97–105.
- Moray, N., 1959. Attention in dichotic listening: affective cues and the influence of instructions. *Q. J. Exp. Psychol.* 56–60.
- Näätänen, R., Paavilainen, P., Rinne, T., Alho, K., 2007. The mismatch negativity (MMN) in basic research of central auditory processing: a review. *Clin. Neurophysiol.* 118, 2544–2590.
- Näätänen, R., Jacobsen, T., Winkler, I., 2005. Memory-based or afferent processes in mismatch negativity (MMN): a review of the evidence. *Psychophysiology* 42, 25–32.
- Näätänen, R., Gaillard, A.W., Mantysalo, S., 1978. Early selective-attention effect on evoked potential reinterpreted. *Acta Psychol. (Amst.)* 42, 313–329.
- Nicol, R.M., Chapman, S.C., Vértes, P.E., Nathan, P.J., Smith, M.L., Shtyrov, Y., Bullmore, E.T., 2011. Fast reconfiguration of high-frequency brain networks in response to surprising changes in auditory input. *J. Neurophysiol.* 107, 1421–1430.
- Nowak, K., Oron, A., Szymaszek, A., Leminen, M., Näätänen, R., Szelag, E., 2016. Electrophysiological indicators of the age-related deterioration in the sensitivity to auditory duration deviance. *Front. Aging Neurosci.* 8, 1–10.
- Pekkonen, E., Rinne, T., Reinikainen, K., Kujala, T., Alho, K., Naatanen, R., 1996. Aging effects on auditory processing: an event-related potential study. *Exp. Aging Res.* 22, 171–184.
- Peter, V., McArthur, G., Thompson, W.F., 2010. Effect of deviance direction and calculation method on duration and frequency mismatch negativity (MMN). *Neurosci. Lett.* 482, 71–75.
- Pillsbury, W.B., 1908. *Attention*. Swann, Sonnenschein, London.
- Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. *Clin. Neurophysiol.* 118, 2128–2148.
- Raz, N., Gunning, F.M., Head, D., Dupuis, J.H., McQuain, J., Susan, D., Briggs, Wendy, J., Loken, A.E.T., Acker, J.D., 1997. Selective aging of the human cerebral cortex

- observed in vivo: differential vulnerability of the prefrontal gray matter. *Cereb. Cortex* 7, 268–282.
- Recasens, M., Leung, S., Grimm, S., Nowak, R., Escera, C., 2015. Repetition suppression and repetition enhancement underlie auditory memory-trace formation in the human brain: a MEG study. *Neuroimage* 108, 75–86.
- Rinne, T., Alho, K., Ilmoniemi, R.J., Virtanen, J., Näätänen, R., 2000. Separate time behaviors of the temporal and frontal mismatch negativity sources. *Neuroimage* 12, 14–19.
- Romanski, L.M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P.S., Rauschecker, J.P., 1999. Dual streams of auditory afferents target multiple domains in the primate prefrontal cortex. *Nat. Neurosci.* 2, 1131–1136.
- Ruzzoli, M., Pirulli, C., Brignani, D., Maioli, C., Miniussi, C., 2012. Sensory memory during physiological aging indexed by mismatch negativity (MMN). *Neurobiol. Aging* 33, 625.e21–625.e30.
- Sallinen, M., Lyytinen, H., 1997. Mismatch Negativity during objective and subjective sleepiness. *Psychophysiology* 34, 694–702.
- Schröger, E., Marzecová, A., Sanmiguel, I., 2015. Attention and prediction in human audition: a lesson from cognitive psychophysiology. *Eur. J. Neurosci.* 41, 641–664.
- Sowell, E.R., Peterson, B.S., Thompson, P.M., Welcome, S.E., Henkenius, A.L., Toga, A.W., 2003. Mapping cortical change across the human life span. *Nat. Neurosci.* 6, 309–315.
- Theeuwes, J., 2019. Goal-driven, stimulus-driven, and history driven selection. *Sciencedirect. Curr. Opin. Psychol.* 29, 97–101.
- Todorovic, A., van Ede, F., Maris, E., de Lange, F.P., 2011. Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: a MEG study. *J. Neurosci.* 31, 9118–9123.
- Walhovd, K.B., Fjell, A.M., 2001. Two- and three-stimuli auditory oddball ERP tasks and neuropsychological measures in aging. *Neuroreport* 12, 3149–3153.
- Wronka, E., Kaiser, J., Coenen, A.M.L., 2008. The auditory P3 from passive and active three-stimulus oddball paradigm. *Acta Neurobiol. Exp. (Wars)*. 68, 362–372.